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THE UNIVERSITY OF ALBERTA

LIFE TABLES FOR SOME NATURAL POPULATIONS OF CHIRONOMIDAE (DIPTERA) IN A TYPHA MARSH

BY

© VICTOR J.E. McCAULEY

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Life Tables for Some Natural Populations of Chironomidae (Diptera) in a Typha Marsh" submitted by Victor J.E. McCauley in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Aquatic Insect Ecology.

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ABSTRACT

A study was made of some field populations of Chironomidae occurring in an isolated pure stand of cat-tail (Typha latifolia L.) in George Lake, Alberta. The habitat was sampled from May, 1973 to September, 1974. Sampling of all developmental stages of the chironomids revealed that there were four common species, viz. Dicrotendipes nervosus (Staeger), Glyptotendipes dreisbachi Townes, G. lobiferus (Say) and G. nr. paripes Edwards. The former species was univoltine and the others were bivoltine.

Life tables were constructed for two consecutive cohorts of G. lobiferus and of G. nr. paripes and for one of each of the other two species.

A generalized survivorship curve was constructed using the data from all six cohorts. Despite the fact that the cohorts varied in length from approximately 3-13 months, and had starting densities which differed by up to a factor of four, there was only moderate spread in the data. The generalized curve indicates that 1) by completion of only 20% of the duration of the cohort only approximately 10% of the initial population is still alive, 2) for approximately the subsequent 60% the mortality rate is low; and 3) for the final 20% it is high. The range in the per cent of the populations which survived to the adult stage was 0.05 - 8.21%.

The maximum value recorded for the intrinsic rate of natural increase was 0.0380, and was obtained for a summer cohort of G. lobiferus. A value approximately five times smaller was obtained for its overwintering cohort.

Although the degree to which the three cogeneric species competed is unknown, there was evidence of their ability to co-exist through niche specialization, as indicated by morphological character displacement and by different spatial utilization of the sub-habitats.

Dormancy appeared to be involved in the life-cycle of G. lobiferus.

A key is given to differentiate the three species of Glyptotendipes in all seven developmental stages and in both sexes.

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I am indebted also to Dr. J. C. Holmes, Department of Zoology, University of Alberta, for his help in identifying some of the chironomid parasites, and especially for his stimulating comments concerning interpretation of the data.

Thanks are due also to Dr. B. Chernik, Department of Zoology, University of Alberta, for advice on statistical matters, and for writing the computer programme for transforming the data. Similarly, I thank Dr. S. Zalik, Department of Plant Science, University of Alberta, for advice on statistical matters.

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I. INTRODUCTION

The Chironomidae is an ecologically diverse family of insects which is world wide in distribution, and which frequently constitutes a major component of the invertebrate fauna of rivers, lakes and streams.

In reviewing the literature on this group, Mundie (1957) concluded that the study of chironomids has followed two main lines which may be termed the limnological and the entomological. One has been concerned with the distribution of different kinds of chironomids in different lakes, with the association of these with lake types, and with the numbers and weights of chironomids as aspects of lake productivity. The other has dealt with various aspects of the biology of particular species, such as their feeding habits, respiration, voltinism, etc. During the 17 years since Mundie's review there has been a decrease in the degree of study which certain of these aspects have received and an increase in that of others; however, the basic statement essentially still holds.

In the case of studies on chironomid population dynamics, there appears to be none which has dealt with all seven developmental stages (egg, four larval instars, pupa and adult); in fact, because of the large mesh size that frequently is employed in sieving the samples, larval density estimates may not include specimens in the first or in the first and second instar. Although these data are of value, e.g. in estimating productivity, they are inadequate to permit a detailed understanding of the population dynamics of the

species. Such an understanding necessitates an intensive study censusing the change in abundance of all the developmental stages of a population at one place. From these data a life table may be constructed for each cohort and, from all of these, various estimates made, such as the period(s) in the life cycle when mortality is greatest, the proportion of the population surviving to reproduce, etc. If, concurrently, data are gathered on the species' parasites, the abundance of other species in the habitat and on various abiotic factors, then an assessment may be made also of the possible role of each in influencing the shape of the survivorship curve. Subsequently, hypotheses may be developed for testing, both in the study area and in other geographical localities. Such results can contribute significantly to the understanding of the evolutionary ecology of a species, and to the determination of the patterns in ecology.

In view of the above listed potential value of the data, the purpose of the present study was the construction of life tables, calculation of the various population statistics, and determination of the relative importance of at least some of the mortality factors for some natural field populations of Chironomidae.

George Lake, Alberta (53°57'N, 114°06'W) was chosen as the study site as it is in close proximity to and easily accessible from the Department of Entomology field station. To meet the requirements for construction of life tables a search was made of the lake for a suitable study area. This resulted in the choice of a stand of cat-tail (Typha latifolia L.). This choice was made because (1) it is an

isolated pure stand; (2) various species of chironomids were found in the live and in the dead plant shoots and on the lake bottom, thereby permitting a comparison of different microhabitats; and (3) some of the chironomids were parasitized, primarily by Mermithidae (Nematoda), thus permitting an assessment of the importance of parasitism as a mortality factor. Additionally, since T. latifolia is world wide in distribution, results obtained in the present study can be tested in other geographical localities.

II. THE STUDY AREA

A map showing the location of George Lake, the study area and the Department of Entomology field station is given in Fig. 1.

A map of the study area is given in Fig. 2. The stand of Typha covered an area of 54 m^2 and was completely isolated from other emergent aquatic vegetation. The nearest Typha was approximately 7.5 m west; it joined the shoreline and, to the north, joined a stand of Scirpus validus Vahl., which was located approximately 10 m from the study area. These two species of plants formed a continuous band 10-15 m wide which completely enclosed the study area to the west and to the north, and which joined with the shoreline approximately 200 m to the east. This, combined with the heavily wooded shore, resulted in the Typha stand being well protected from wind and wave action.

Throughout 1973 the water depth in the Typha stand was 50-55 cm, and the stand was located 0.5-1.0 m from the shoreline. In 1974 the water depth was 72-122 cm, and the distance of the stand from the shoreline varied up to a maximum of approximately 40 m.

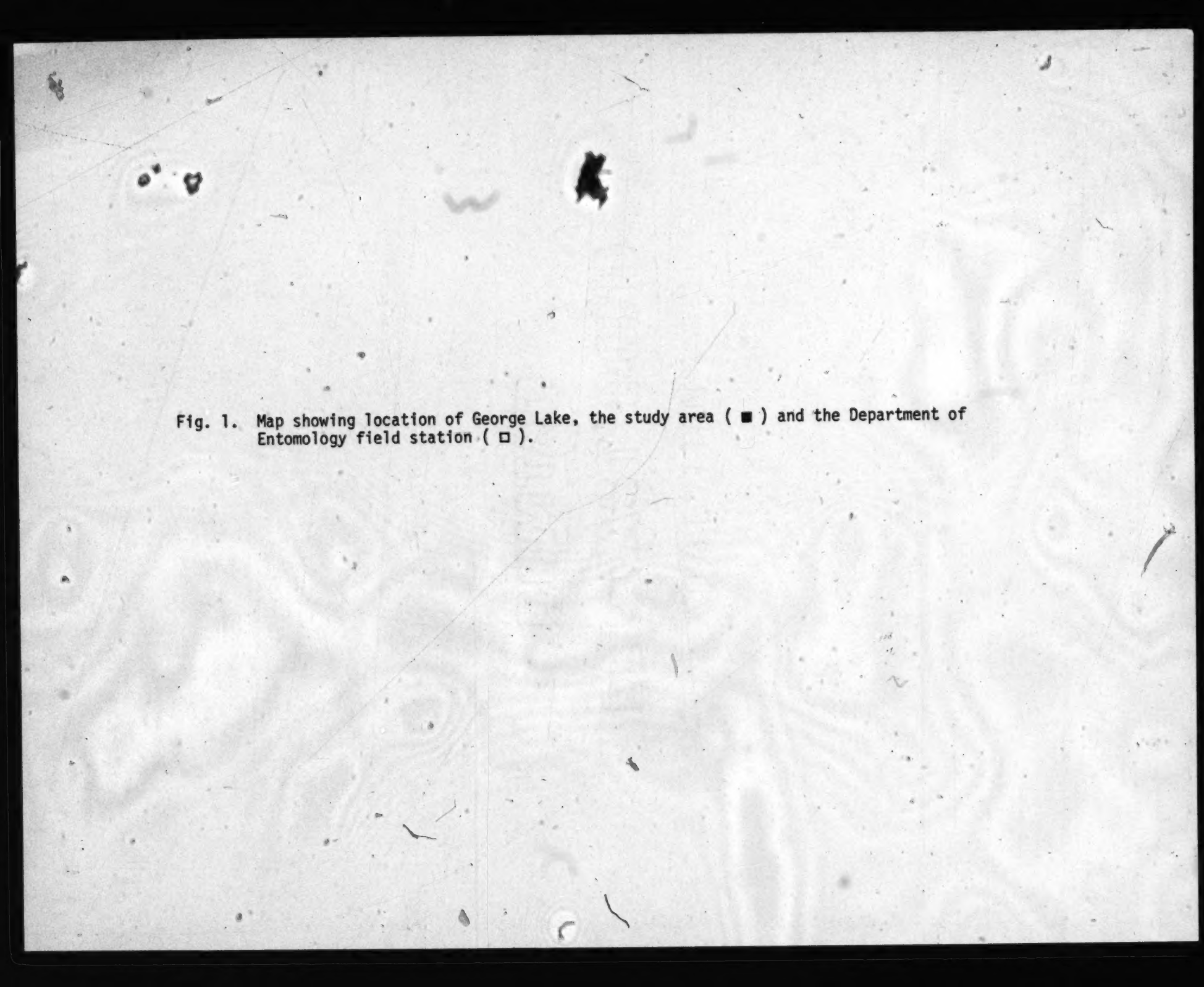
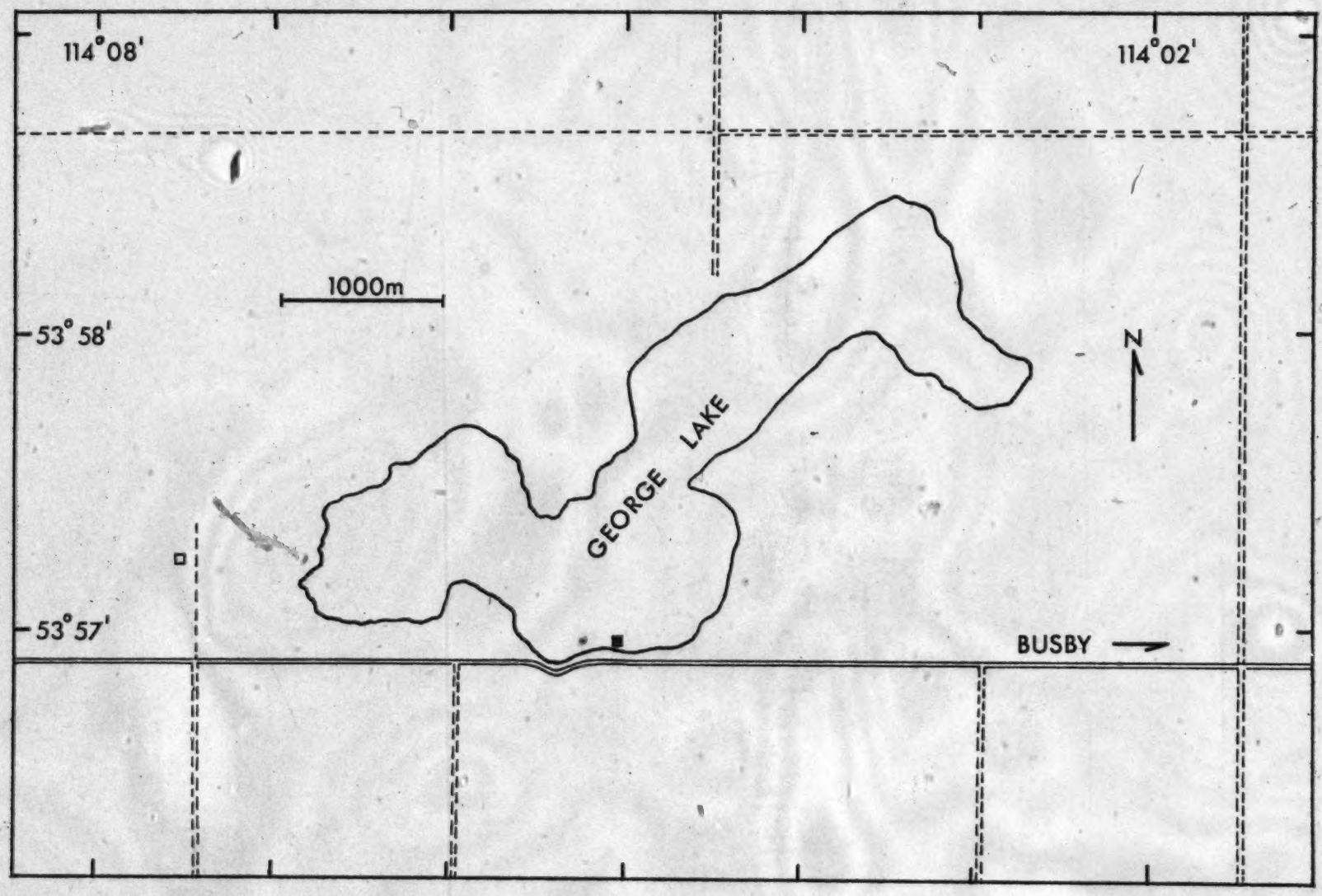


Fig. 1. Map showing location of George Lake, the study area (■) and the Department of Entomology field station (□).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1000m
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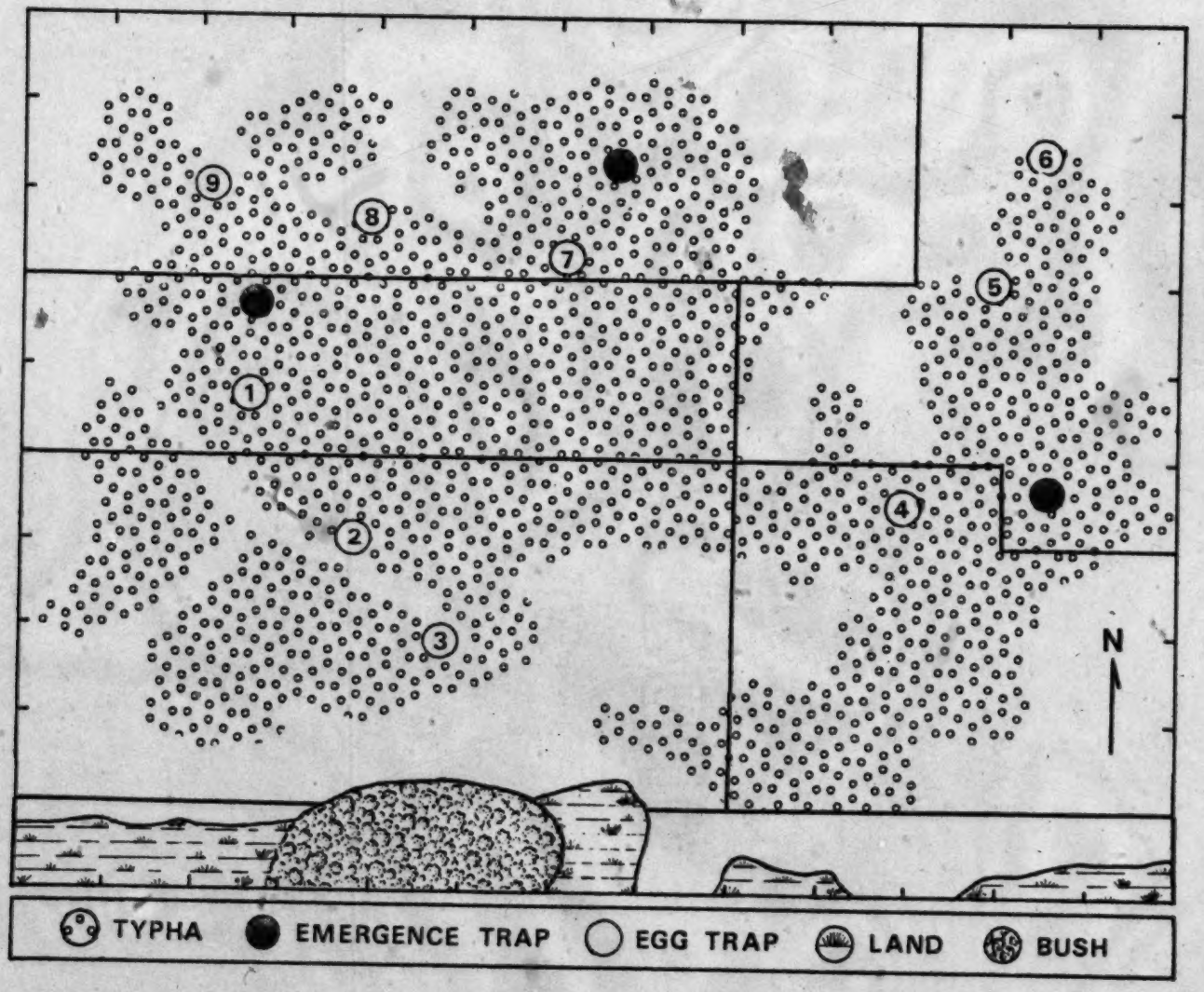
53°57'
GEORGE LAKE
N
BUSBY

Fig. 2. Map of stand of Typha latifolia showing location of egg traps and emergence traps, and the delimitation of the five sampling quadrats. The divisions on all sides of the map each represent one meter.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5
1
2
3
4
N
TYPHA
EMERGENCE TRAP
EGG TRAP
LAND
BUSH

III. METHODS

A. Surveying of Study Area.

At the beginning of May, 1973, i.e. shortly after all ice had melted, a map was made of the Typha stand. This entailed determination of the area, subdivision into units of 1 m^2, and determination of the number of dead plant shoots in each. Determination of the number of live plant shoots in the entire stand of Typha was made at the beginning of June, in mid-July and mid-August, and at the end of September, 1973.

B. Physical Parameters.

Accompanying each survey, and on each date biological samples were collected, the water depth, and vertical temperature and transparency profiles were recorded at the edge of the Typha near egg trap #1 (Fig. 2). This resulted in measurements being made every 4-5 days during both summers, weekly during the fall, and on four occasions during the winter. Transparency was measured using a Secchi disc, and temperature using a Laboratory Thermometer Model BAT-4 and a Type OT-1 probe (Bailey Instrument Co. Inc., Saddle Brook, New Jersey).

C. Biological Sampling.

1. Eggs.

To determine the number of eggs laid by each species of chironomid in the study area, egg traps (Fig. 3) were positioned in the stand of Typha at the beginning of May, 1973. Initially, six egg traps were employed, but three more were added on June 13 (Nos. 1-6 and Nos. 7, 8 and 9 respectively in Fig. 2).

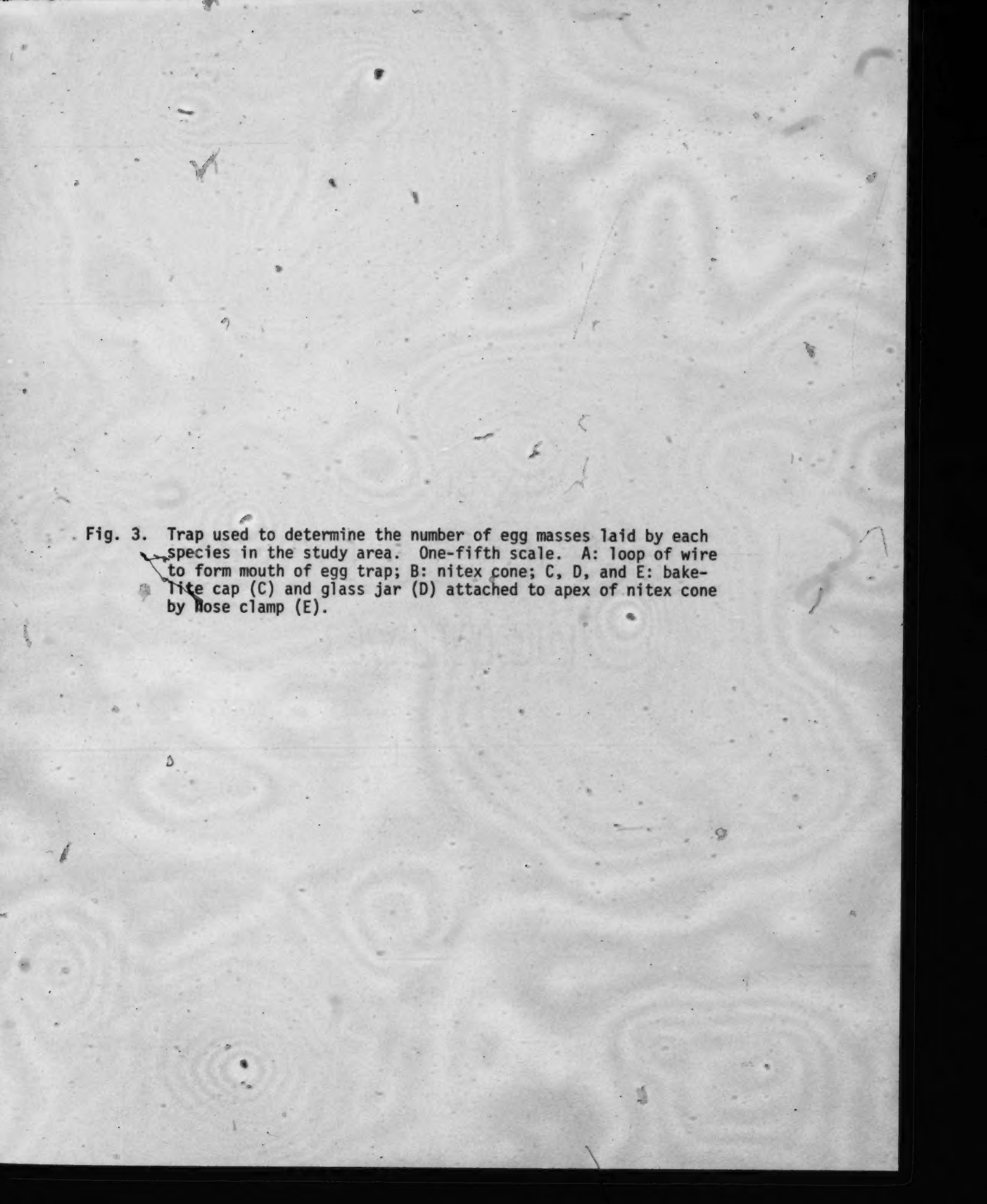
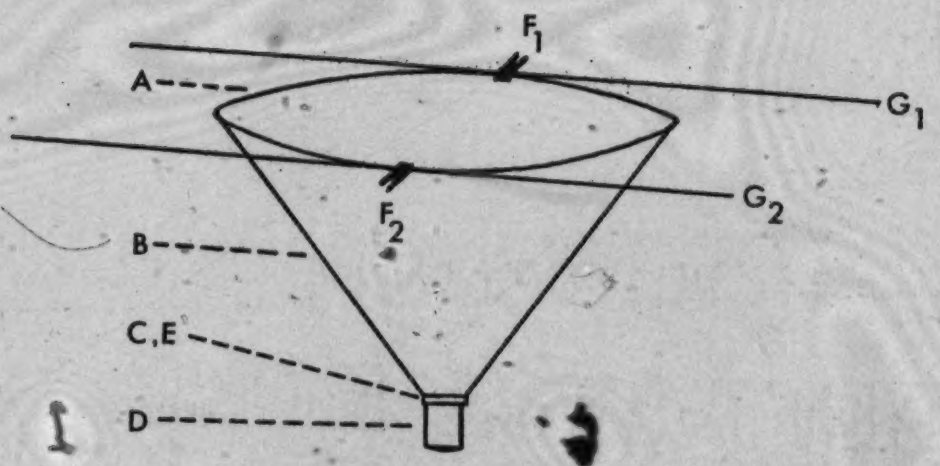


Fig. 3. Trap used to determine the number of egg masses laid by each species in the study area. One-fifth scale. A: loop of wire to form mouth of egg trap; B: nitex cone; C, D, and E: bakelite cap (C) and glass jar (D) attached to apex of nitex cone by hose clamp (E).


F1
A
G1
G2
F2
B
C,E
D

Each egg trap (Fig. 3) consisted of a loop of stainless steel wire (A), approximately 0.5 cm thick, which was attached to the base of a cone of Nitex[1] (B), 25 cm tall and open at the apex. The base diameter of the cone was 35.8 cm, and thus the base area was 0.1 m^2. A bakelite cap (C), 5 cm in diameter, from a 6 oz glass jar (D) was placed upside-down in the open apex of each cone and held in position by means of a hose clamp (E). A hole 3 cm in diameter was cut in the bakelite cap.

Each egg trap was suspended 1-2 cm below the water surface in the stand of Typha by attachment with clothes-pegs (F_1,F_2) to pairs of nylon ropes (G_1,G_2) running between wooden crosses embedded in the sediment. The weight of the hose clamp, glass jar and bakelite cap was sufficient to keep the nitex cone inverted and taut.

For examination of an egg trap, the clothes-pegs were removed and the trap gently lifted out of the water. Any egg masses attached to the nitex were washed down into the glass jar. Subsequently, the jar was unscrewed, capped with a numbered lid, and taken back to the laboratory where the contents were examined for egg masses under a microscope at 6X. Any pieces of plant or debris found floating within the area encompassed by the base of the egg trap also were collected and examined microscopically for egg masses.

The egg traps were examined and emptied essentially every two days. They were removed from the study area at the beginning of October, 1973, approximately two weeks after the last adult emerged.

---

[1] A synthetic bolting cloth manufactured by Tobler, Ernst & Traber, Inc., New York.

2. Larvae.

a) Larvae associated with emergent vegetation. These larvae were collected using a sampler (Fig. 4) consisting of an aluminum base (A) into which is screwed a piece of transparent acrylic tubing (B). A brass plate (C) is machined to slide smoothly along a groove cut on the inside of each side of the aluminum base. Attached to the brass plate is a stainless steel rod (D) which passes through a hole (E) in the base. A spring (F) is located on the rod between the brass plate and the end of the aluminum base. The length of the spring is such that it is slightly compressed when the brass plate seals the bottom of the acrylic tube (B). At the end of the brass plate also is located a hole (G) which bisects hole E in the vertical plane.

To sample, the brass plate is pulled backwards to the maximum compression of the spring and a stainless steel trigger (H), is fitted into hole G and down into a notch in rod D. The plant shoot to be sampled is cut off gently at the air-water interface and the sampler quickly lowered into the water around it. When the bottom of the sampler reaches the mud-water interface, trigger H is pulled out. This releases the brass plate which cuts off the plant and seals the bottom of the sampler. The sampler then is lifted out of the water, the plant placed in a container, and the contents of the sampler filtered through a 156 μ mesh sieve. The residue in the sieve is washed into a separate container.

For sampling shoots in water of a depth greater than the length of the acrylic tubing, another piece may be attached by means of the threaded aluminum collar (J).

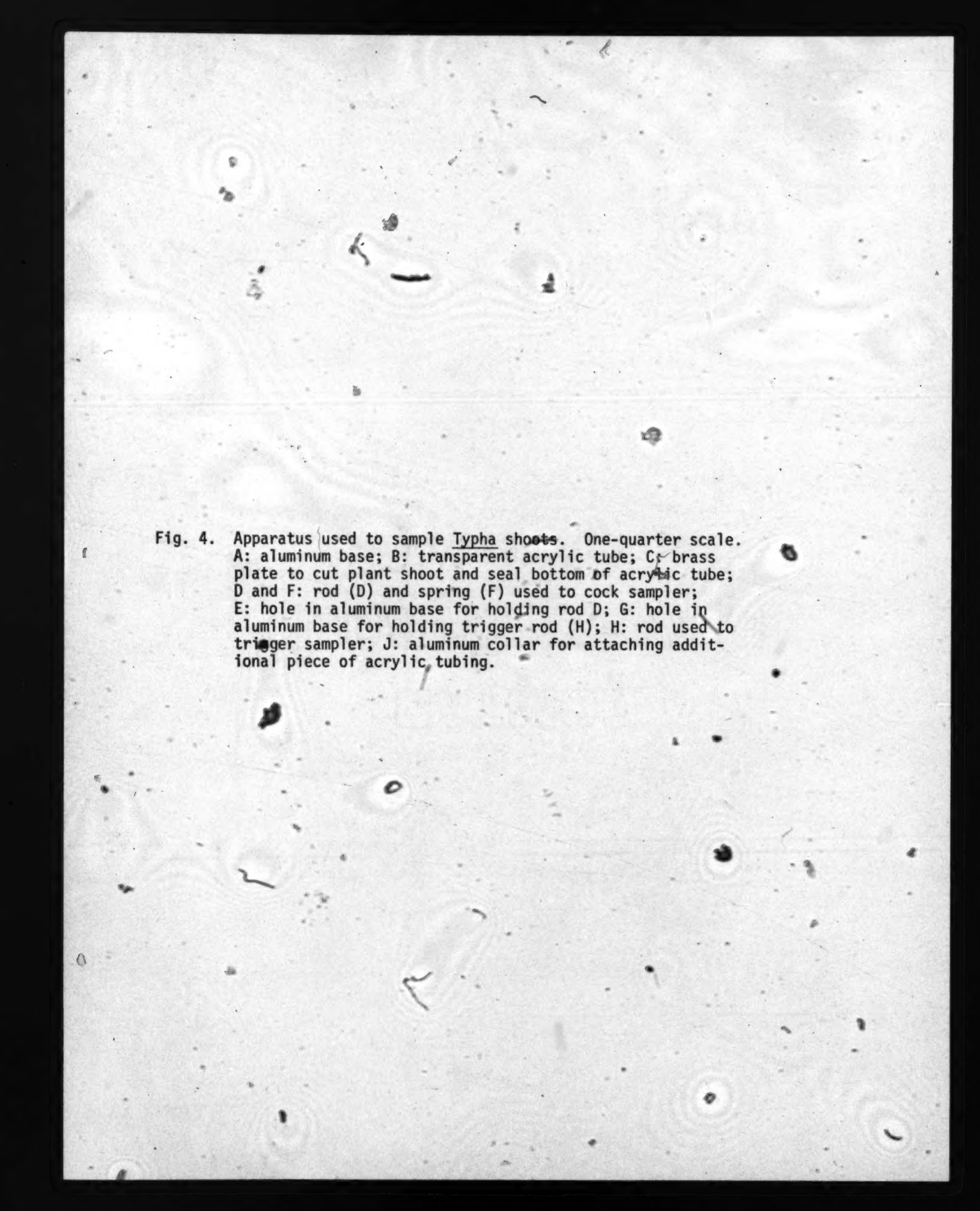
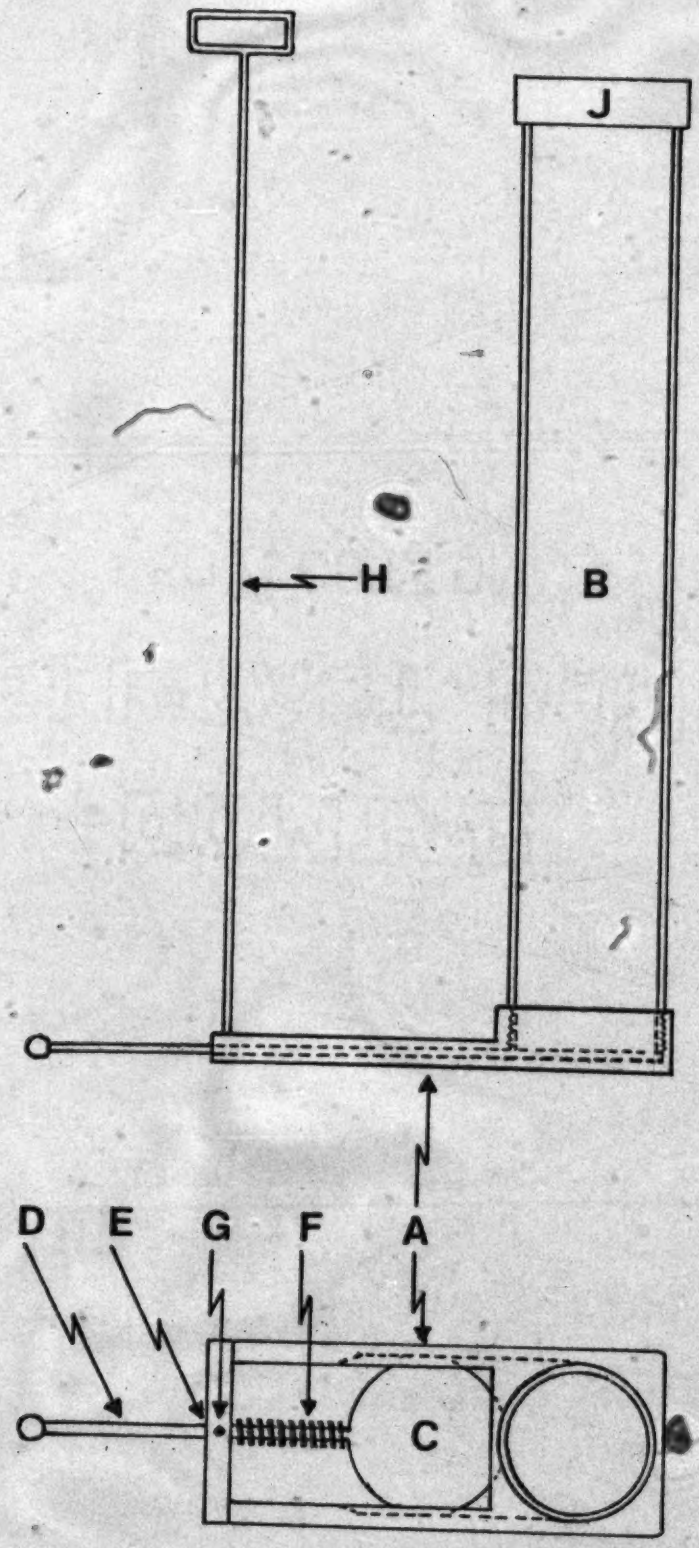


Fig. 4. Apparatus used to sample Typha shoots. One-quarter scale. A: aluminum base; B: transparent acrylic tube; C: brass plate to cut plant shoot and seal bottom of acrylic tube; D and F: rod (D) and spring (F) used to cock sampler; E: hole in aluminum base for holding rod D; G: hole in aluminum base for holding trigger rod (H); H: rod used to trigger sampler; J: aluminum collar for attaching additional piece of acrylic tubing.


J
H
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C

On collection, all plant samples were placed in individual plastic bags and stored live in an ice chest containing cold (ca. 12°C) water (from a small shaded stream near the study area). During warm weather the water was kept cool by the addition of ice. Immediately on returning to the laboratory the plant samples were placed in a refrigerator (4 ± 0.5°C). All plant samples were sorted live under a microscope at 6-50X, this usually being completed the day after collection.

On extraction, all chironomid larvae were killed and preserved by freezing. All other invertebrates were killed and preserved with 70% ethanol.

b) Larvae on lake bottom. These larvae were collected using a modified Kajak corer (Kajak, 1965) which had a bite of 15.9 cm^2. Core samples were treated similarly to the plant samples except that they were placed unsieved in plastic bottles on collection, and were frozen immediately on returning to the laboratory. When ready for analysis, core samples were thawed at room temperature, sifted through a 180 μ mesh sieve, and also examined under a microscope at 6-50X.

On extraction, all chironomid larvae were re-frozen and all other invertebrates preserved in 70% ethanol.

The technique of preservation of the chironomid larvae from the plant and core samples by freezing is considered superior to that involving usage of standard zoobenthos preservatives, such as formalin or ethanol. Freezing retains the natural plasticity of the larvae, thereby permitting easy orientation of the specimens for measurement. Additionally, it retains the natural transparency of the larvae, thereby eliminating, in most instances, the necessity to clear the

head capsule with potassium hydroxide to permit identification. Retention of the natural transparency also greatly facilitates examination of the larvae for parasites.

Collection of larvae by methods a) and b) was done in a stratified random manner. On determination of the number of dead plant shoots in the entire Typha stand at the beginning of May, 1973, based on units of 1 m^2 it was divided into five quadrats, so that each contained approximately equal numbers of plant shoots. This resulted in the Typha covered portion of the quadrats also being approximately equal in area. Subsequently, approximately equal numbers of live Typha shoots developed in each quadrat.

Each unit of 1 m^2 in each quadrat was assigned a number, and the choice of the unit in which samples were to be collected on each sampling date was determined using a table of random numbers. The absence of any marked inter-quadrat differences in area, or in the number of live or dead plant shoots within each, resulted in the live and the dead plant shoot samples, and in the core samples, all being collected essentially in a proportional stratified random manner.

Both plant and core samples usually were collected at intervals of five days throughout the summer, but less frequently in fall and winter 1973, and in spring 1974.

On each sampling date an entire plant shoot (portion between the air-water- and the mud-water-interface) and a core was collected from each of the four randomly chosen quadrats. All samples were collected from a boat. Each quadrat was sampled on four of every five consecutive sampling dates. Initially only dead

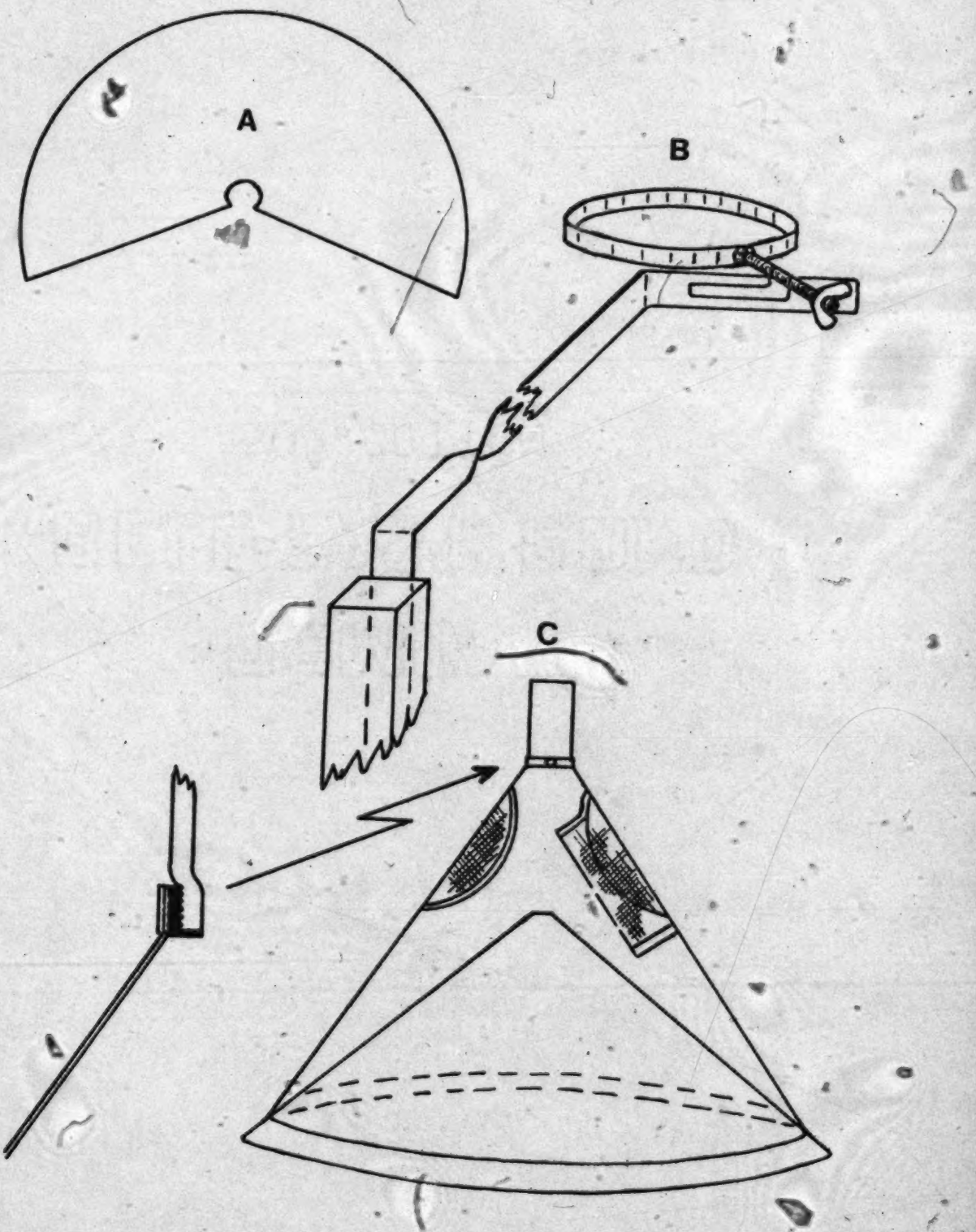
plant shoots were present; however, when the new growth appeared, four live shoots also were collected from the same quadrats as the dead shoots on each sampling date.

3. Adults.

To determine the emergence patterns and the number of specimens of each species successfully completing the aquatic phase of the life cycle, emergence traps were placed in the Typha stand at the beginning of May, 1973 and 1974 (Fig. 2). Since many of the larvae occurred in the plant shoots, only an emergence trap positioned at the air-water interface could be employed. None of those currently in use was considered satisfactory for one or more reasons, consequently a new design was developed.

a) Construction of emergence trap. The new emergence trap (Fig. 5) is constructed from 0.02" thick transparent vinyl plastic, cut to the shape of a circle with an arc, approximately two-fifths its size removed (Fig. 5A). Construction of the cone is accomplished by overlapping the two radial edges 1-2 cm, holding them in position with 3-4 thumb tacks, and bonding by the application of ethylene dichloride to the junction. Bonding is complete within 5-10 minutes. The apex of the cone is warmed over a flame and an 8 oz screw-top glass jar is slowly pushed through, bottom first, from below, thereby producing a collar. A circular hole, 4.5 cm in diameter, is cut in the 6 cm bakelite cap from the glass jar, and the cap is placed upside-down in the neck of the cone. It is held in this position by a hose clamp, to which a threaded bolt has been silver soldered (Fig. 5B). A second cone, also made from the transparent vinyl plastic, is constructed in

Fig. 5. Trap used to determine the emergence pattern and the number of specimens of each species of chironomid successfully completing the aquatic phase of the life cycle. A: shape of plastic used to construct trap (one-quarter scale); B: hose clamp used to hold glass jar in position at apex of trap. Soldered to the hose clamp is a bolt for attaching the emergence trap to a stake in the study area (three-quarter scale); C: emergence trap (one-quarter scale).


A
B
C

a similar manner, but with a hole 3 cm in diameter at its apex. The apical angle of the latter cone is greater than that of the former, thereby permitting the positioning of one on top of the other (Fig. 5C).

The lower cone covers an area of 0.1 m^2. To bond the two cones together, one is placed on top of the other and ethylene dichloride added to the junction. To strengthen the bond, and to eliminate the apex of the very acute angle at the point of bonding, a viscous solution of the acrylic plastic dissolved in ethylene dichloride is added to the inside.

Two holes, each approximately 10 cm in diameter, are made in the upper cone near its apex by means of a hot metal lid. One is covered with a circle of nitex which is bonded to the acrylic plastic using waterproof glue. The other is covered with the same material but cut to the shape shown in Fig. 5C and bonded to the plastic only at the top. The lower edge of the nitex is attached to the trap by means of a piece of waterproof adhesive tape. The purpose of the holes is to permit circulation of air within the trap and hence minimize condensation, as the consequent shading might influence the behavior of the ascending pupae. The adhesive tape permits access to within the trap if necessary.

To operate, the bolt soldered to the hose clamp is fitted into a groove machined in a metal rod and the trap is held in position by a wing nut. The metal rod, approximately 50 cm long, is attached to a stake driven into the sediment (Fig. 5B). The trap is positioned with its base 2-3 cm below the water surface.

To service, the wing nut is loosened and the trap removed from

the water. A rubber bung is inserted in the hole at the apex of the lower cone to prevent escape of any specimens. Insects within the trap are killed by spraying them with dilute alcohol (ca. 30%) through the nitex windows, and then are drained into the jar at the top of the trap. The jar is unscrewed, the rubber bung removed and the trap rinsed out with water. A new jar is screwed into the top of the trap and the trap repositioned in the water.

b) Efficiency of emergence trap. Two types of efficiency can be determined for an emergence trap, viz. trapping efficiency and retention efficiency. The former is the ratio of the number of individuals emerging inside a trap to the number which would have emerged there had the trap had no attractive or repulsive effect. Thus the value may range from zero to above unity. The latter is the ratio of the number of individuals in a trap after a given period of time to the actual number which entered it. Thus the value may range from zero to unity. As various physical parameters can influence both types of efficiency, experiments were performed in the laboratory.

i) Trapping efficiency. A plastic swimming pool, 2.4 m in diameter, was filled to a depth of 40 cm with lake water, and mud-water interface sediment, which had been sifted through a 250 μ mesh sieve, added until a uniform layer approximately one centimeter thick was obtained. A conical framework consisting of 10 stainless steel rods, each approximately 0.4 cm in diameter, and with a base diameter of 2.4 m, was placed on the swimming pool and covered with 6 mil thick transparent polythene film. The polythene was attached to the top of the swimming pool and a window, 250 x 20 cm, was cut out at the base

of the polythene tent. An additional window, 15 cm in diameter, was cut out at the apex of the tent. Both windows were covered with 0.75 mm nitex. The windows were necessary to completely eliminate condensation on the inside of the tent. Access to within the tent was achieved via a longitudinal slit in the polythene.

Chironomid egg masses were collected in the field, identified to species, and those of each species distributed as uniformly as possible on the bottom of the swimming pool.

The water in the swimming pool was kept oxygenated by two aerators suspended in the water column, their position being moved every day. During determination of the efficiency of the emergence trap the aerators were switched off to eliminate the production of currents; however, the water was aerated every one or two days for a few hours. Very few specimens emerged during this period, and any which did were discarded.

Illumination was provided by a bank of six fluorescent lights directly above the swimming pool, and was run on a 12/12 hour light/dark cycle.

The emergence traps were positioned in the swimming pool as shown in Fig. 6. The position was altered each time the traps were emptied, but traps T_1, T_2, and T_3 always were in contact with the edge of the swimming pool, and traps T_4, T_5, and T_6 never so. An attempt was made to keep each trap equidistant from the two nearest it.

The trapping efficiency was determined over a period of 21 days. Collection of all chironomid adults from within the polythene tent and from each of the six emergence traps was made every two days, except

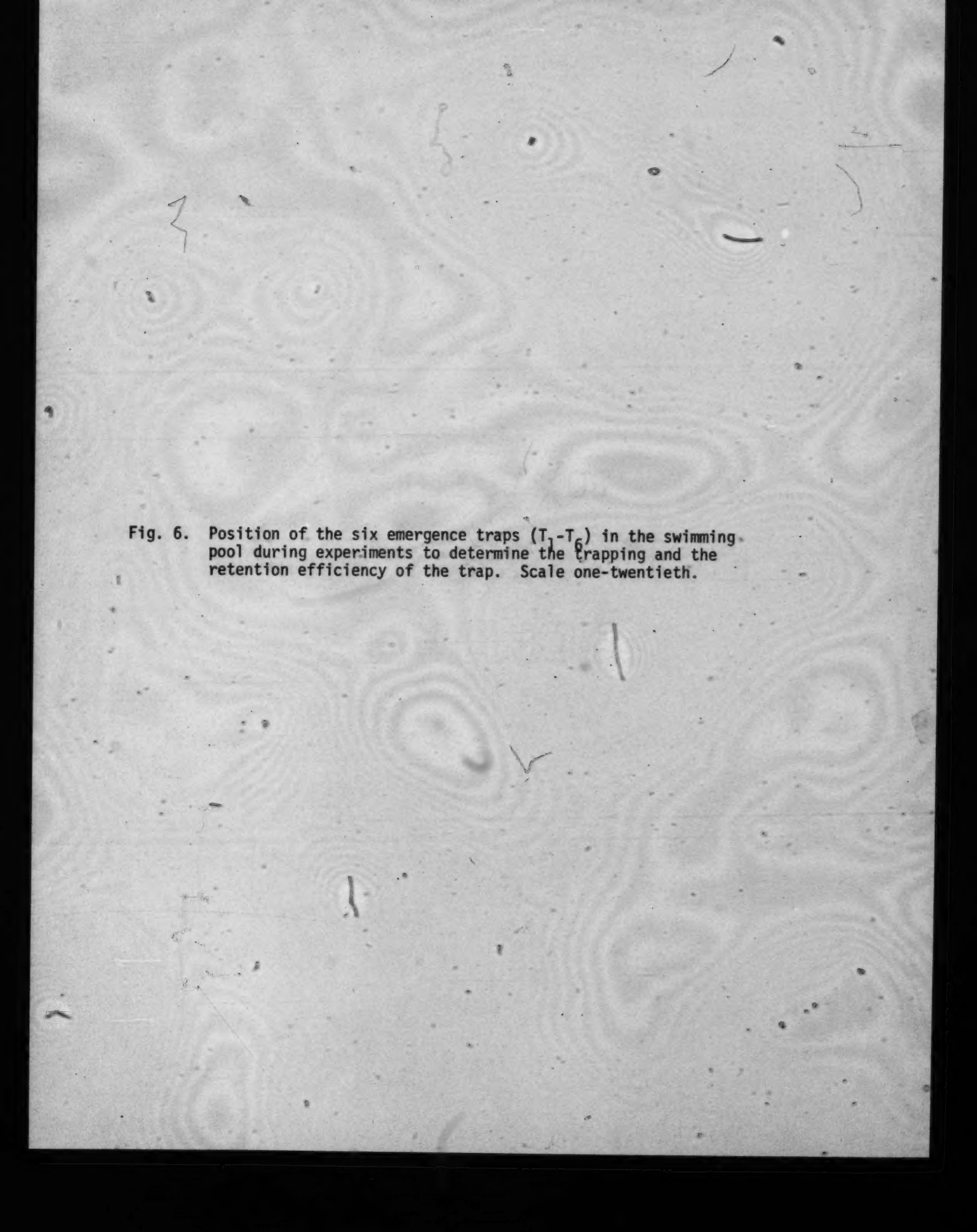
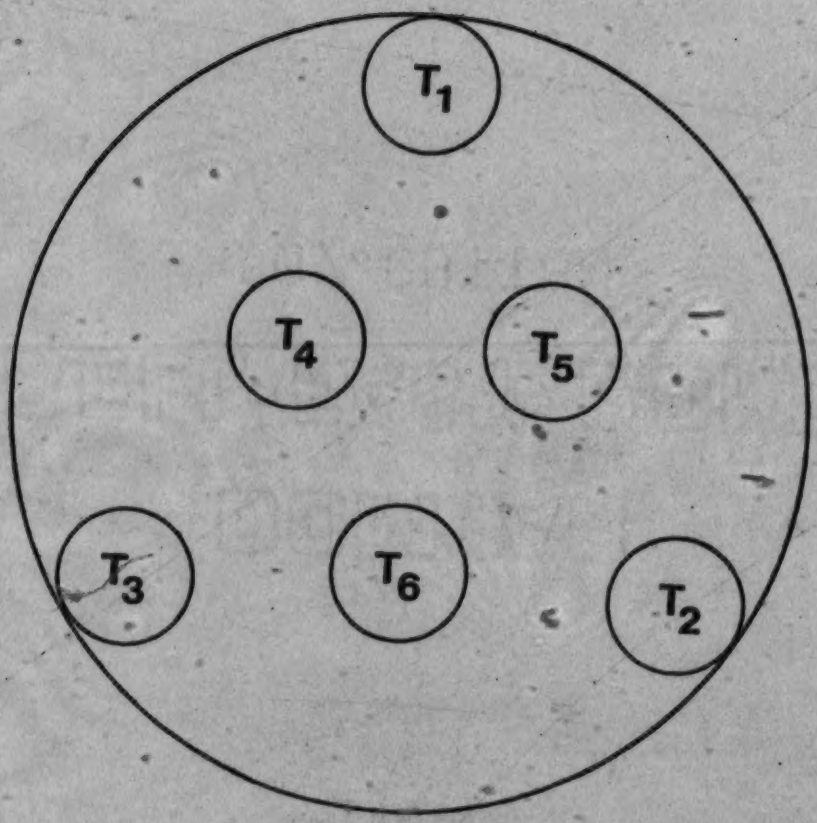


Fig. 6. Position of the six emergence traps (T_1-T_6) in the swimming pool during experiments to determine the trapping and the retention efficiency of the trap. Scale one-twentieth.


T1
T4
T5
T3
T6
T2

for the final collection, which was made after an interval of three days. Additionally, on each collection date the water surface was examined for adults.

ii) Retention efficiency. As the retention efficiency of a trap could depend on the rate and number entering, and on the sex ratio of the specimens trapped, experiments were of two types. One set involved adding a known and constant number of adults to a trap each day, and the second set involved adding a known number just at one specific time. In both sets of experiments the sex ratio was maintained constant at unity, and the traps were examined each morning. Specimens found floating on the water enclosed by the base of the trap either were dead or were unable to leave the water. Since these specimens could become waterlogged and sink, and/or be consumed by predators under field conditions, they were assumed "lost" and represented a decrease in retention efficiency. In both sets of experiments the adults added to the traps were a maximum of one day old.

The experimental design used for determining the trapping efficiency was employed for these experiments also. The only difference was that the base of each emergence trap was covered with a piece of transparent polythene film. This prevented the entrance of any emerging chironomids, and ensured retention of all "lost" adults. Additionally, all emergence traps were left in the one position.

Experiments dealing with the number of specimens constantly added to an emergence trap each day covered a theoretical emergence rate of 20-100/m^2/day. Those dealing with the number added just at one specific time covered a theoretical emergence rate of 20-440/m^2/day. Each of the former experiments was terminated after seven days, as this was

considered the maximum interval most investigators leave emergence traps in the field before emptying. Each of the latter experiments lasted on average for five days, as this was the average time taken for all adults to die.

For all efficiency experiments with the emergence trap, the average air and water temperature was 25°C (range, 24-26°), and the average relative humidity was 84% RH (range, 80-90).

All experiments were conducted with G. lobiferus as only its egg masses were common when it was decided to start the experiments.

Two types of statistical tests were performed on the data, viz. paired t-tests and Chi-Squared tests. All data analyzed using the paired t-test were checked for agreement with a Poisson series at $P < 0.05$ (Elliot, 1971, p. 42) and normalized using the appropriate transformation (Elliot, 1971, p. 33) prior to performing the test.

D. Density of Each Species of Chironomid.

In the present study three sub-habitats were samples, viz. live plant shoots, dead plant shoots and the lake bottom. Because of the intra- and inter-quadrat variation in size of the live and dead plant shoots, it was necessary to obtain a common unit of measurement which would permit a summation of the density of larvae of a species in each of these sub-habitats. Additionally, it was necessary that this resultant combined density could be summed with the density on the lake bottom, so that the overall density of a species could be expressed in the most meaningful way, viz. number per square meter.

The number of Typha-inhabiting larvae per square meter was

determined according to the following formula: No. of shoots/m^2 x Mean volume/shoot x No. of larvae/plant volume = No. of larvae/m^2. To calculate the first term the number of live and dead plant shoots in the entire Typha stand was determined as outlined in section A. As the number of live and dead plant shoots removed on each sampling date was known also, combination of these data permitted determination of the mean number of live and of dead plant shoots per square meter present in the Typha stand on each sampling date.

As the volume of the sampled portion of live plant shoots (portion between air-water- and mud-water-interface) would increase due to growth, and that of the dead plant shoots could decrease due to decomposition, and/or consumption by detritovores, it was necessary to determine the magnitude of these changes. Consequently, the mean shoot volume was determined for the live and the dead shoots on each sampling date. Calculation of the correlation coefficient of each with time revealed no significant relationship ($P \leq 0.05$). Thus the second term in the equation may be considered constant. Additionally, as there was no significant difference between the mean volume of the live and the dead shoots, the second term was derived by determining the mean volume of all plant shoots collected throughout the study. This gave a value of 251 cc, termed a Standard Plant Volume (hereafter referred to as S.P.V.). Division of the S.P.V. by the volume of a specific plant shoot, e.g. a live shoot, gives a factor by which the number of chironomid larvae of a species associated with that live shoot should be multiplied to determine the number per S.P.V. As the mean number of live shoots per square meter was determined for each

sampling date, multiplication of this value by the number of larvae per S.P.V. gives the mean number of larvae per square meter of live shoots. Similar calculations give a value for the dead shoots; combination of both gives a value for the mean number of larvae per square meter associated with the emergent vegetation.

Determination of the number of larvae on the lake bottom within a square 1 m x 1 m was not corrected to take into consideration the area occupied by the plant shoots. This was not considered necessary as determination of the mean area occupied by live plus dead plant shoots throughout the study gave a mean value of 1.67% of a square meter.

The values given for the total number of larvae of each species per square meter have been derived by summing the number per square meter in the live and in the dead plant shoots and on the lake bottom for each of the four quadrats sampled on each date, and subsequently determining the arithmetic mean of the four.

The 95% confidence limits have been calculated for every density estimate; the method of calculation is given in Appendix III.

During June and July, 1973, no egg masses of G. dreisbachi, G. lobiferus or G. nr. paripes[2] were found in the egg traps. Because of this, and the consequent forced termination of the study if no more were laid by any species in the study area, a search was made for chironomid egg masses at the end of July. This search

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[2] See Appendix I.

revealed a large number of egg masses of G. lobiferus and G. nr. paripes which had been laid approximately 200 m to the east of the study area in a stand of Scirpus validus. A total of 180 egg masses of each species were collected on July 30 and 31, and deposited by hand in a regular distribution in the Typha stand on these two days. All egg masses were identified in the field using a dissecting microscope, and only those containing unhatched eggs were placed in the study area.

During the latter half of August, egg masses were deposited by both G. lobiferus and G. nr. paripes in the study area!

E. Fecundity of Chironomids.

To determine their fecundity, field collected G. lobiferus, and laboratory reared G. lobiferus and G. nr. paripes were cultured individually in 8 oz glass jars containing lake water and a small piece of styrofoam. The laboratory specimens were obtained from the enclosed swimming pool described in Section C. A total of eight field collected and 12 laboratory reared G. lobiferus, and three laboratory reared G. nr. paripes, were cultured but none of the females laid an egg mass before dying. An examination was not made of any other species.

As counts were made of the number of eggs in most egg masses collected throughout the summers of 1972-74, these have been used as an estimate of fecundity. Those egg masses used solely for determination of the egg number were dissolved in a 1% solution of household bleach prior to counting of the eggs. Because of a possible adverse affect on the eggs, this method was not applied to those egg

masses which also were used for rearing. Instead, these egg masses were partially compressed between two glass slides separated by two match sticks prior to counting.

F. Mortality Factors.

To determine the hatching efficiency of the eggs, egg masses collected in the field were identified to species and placed in individual 10 dram glass vials. The top of each vial was covered with a piece of 50 u mesh nitex which was held in place by the plastic snap-cap, the center of which had been removed. These vials were suspended just below the water surface or at the mud-water interface at various localities within the Typha stand. The contents of the vials were examined in the field frequently using a dissecting microscope, and records kept of the ambient water temperature. When no trace could be found of an egg mass, the vial was brought back to the laboratory and its contents examined microscopically at 50X. All unhatched eggs were counted. These were considered dead as none ever hatched after placing in continuously aerated lake water at room temperature (ca. 20°C) for an additional 3-4 days.

In calculating hatching efficiency the mean number of eggs per egg mass for a species as determined in Section E was employed. No attempt was made to count the number of eggs in any of the egg masses used in the experiments, as this might have affected the hatching efficiency.

An examination was made of the role of parasites, and of low water temperature and/or being frozen in ice as possible larval mortality factors.

All larvae collected were examined for parasites at 40-400X.

Records were kept of the identity of each host and of its parasite, and of the percentage parasitism on each sampling date.

Some of the hosts parasitized by mermithid nematodes exhibited the defense mechanism of parasite encapsulation. Consequently, records were kept both of the number of hosts which contained only encapsulated parasites, and those which contained one or more unencapsulated parasites.

To determine the role of low water temperature and/or being frozen in ice as a possible mortality factor, all plant samples collected during the period ice was present on the lake were examined for dead larvae. For examination, each sample was removed from the refrigerator (4 ± 0.5°C) and let stand at room temperature for approximately one hour, or for approximately one hour after all ice had melted. All larvae extracted were placed in a dish containing some of the sample water. Any larvae which did not respond to mechanical stimulation were assumed to have been dead when collected and to have died as a result of exposure to low temperature and/or being frozen in ice.

One of the larvae which did not respond to mechanical stimulation contained a mermithid nematode. It was assumed to have died because of the parasite.

G. Differentiation of Larvae from Overlapping Cohorts.

In George Lake, G. lobiferus has two cohorts per year; one commences about the third week in May and is completed by the end of the summer. The cohort resulting from these adults commences about the first half of August, overwinters, and starts to emerge 2-3 weeks after the ice has melted; however, as emergence continues

throughout the summer, there is a mixing of larvae and adults from the consecutive cohorts.

The methods used for differentiating these larvae (and adults) are given in Appendix I. As very few of the larvae from the preceding cohort were found by the beginning of August (Figs. 16C, 23C), and because of some difficulty in differentiating the morphs thereafter, all fourth instar larvae collected between July 31 and August 15 were assumed to belong to the first cohort in 1973. Thereafter until the end of August all fourth instar larvae collected were very small and consequently were assumed to belong to the second cohort in 1973.

Similar problems in separating larvae of the 1972-73 overwintering cohort of G. dreisbachi and of G. nr. paripes from those of the new cohort of each were not encountered, as essentially none of the overwintering larvae of either species was found after May 30. Separation of the few fourth instar larvae of G. nr. paripes of this first cohort from those of the second cohort was done on the basis of body size as there were two size classes. Because of the results obtained with the G. lobiferus larvae (see Appendix I), the very small larvae were assumed to belong to the new second cohort.

No problems were encountered in the separation of larvae of D. nervosus from consecutive cohorts, as there was usually at least a one instar gap between the minimum age of the overwintering larvae and the maximum age of the new cohort larvae. Additionally, similar body size differences as outlined above were evident.

H. Collection and Rearing of Specimens.

As no data were available on the species of chironomids in

George Lake, and since a basic requisite for the construction of life tables is the accurate differentiation of species in all developmental stages (seven in chironomids, viz. egg, four larval instars, pupa, adult), the first summer also was spent in the regular collecting of egg masses and larvae, especially from the Typha stand and its environs, and rearing these through to the adult (both sexes).

Because of the resultant familiarity gained with the egg masses, species identification of those collected in the egg traps during the summer of 1973 usually was immediately possible; however, those which caused hesitation in identification, or which were unfamiliar, also were reared out.

For rearing, egg masses were placed individually in trays (32 x 19 x 6 cm) containing lake water, sediment, and epiphytic algae which had been scraped off dead Typha shoots, all having been examined microscopically to ensure removal of all macro-invertebrates. The water in each tray was aerated gently and continuously, and periodically some Tetra Min[3] was added. All cultures were examined frequently and some larvae were killed and preserved in 70% ethanol immediately on hatching from the egg, and in each of the three remaining instars. Pre-pupal fourth instar larvae from the cultures, and fourth instar larvae collected in the field, were reared individually in vials containing lake water. Specimens of both sexes were killed in the pupal and in the adult stage, and preserved in 70% ethanol. Notes were made on the coloration of the freshly killed specimens.

[3] A food for tropical fish manufactured by Dr. R.N. Baensch, Melle, West Germany.

I. Preparation, Drawing and Identification of Specimens.

To prepare specimens for drawing and identification, dissected adults, pupae and larvae first were cleared by placing in warm 10% potassium hydroxide for 5-10 minutes and then transferred to glacial acetic acid. The wings, and the legs from one side of each adult, were placed directly into the acetic acid. Subsequently, all were passed through two changes of absolute ethanol and mounted in Euparal[4] under No. 1 coverslips.

All drawings were made using a camera lucida.

The classification of the Chironomidae follows that proposed by Hamilton, Saether and Oliver (1969). Identifications primarily follow Hamilton, Saether and Oliver (In Preparation).

[4]Trademark of G.B.I. (Labs) Ltd., Denton, England.

IV. RESULTS

A. Surveying of Study Area.

When the study area was first mapped on May 8, 1973, 596 dead Typha shoots were present, i.e. a mean density of 11.0 per square meter. On June 3, July 20, August 21, and September 30, 1973, the total number of live Typha shoots in the study area was 820, 870, 874, and 850 respectively. The corresponding mean densities on these dates were 15.2, 16.1, 16.2, and 15.7 per square meter respectively.

B. Physical Parameters.

Throughout 1973 the water depth in the Typha stand was 50-55 cm. An atypically heavy snowfall during the winter of 1973-74 resulted in the water depth increasing to approximately 110 cm following the spring thaw. Subsequently, the water depth decreased slightly; however, considerable rain in late June and in early July resulted in it increasing to 122 cm. Thereafter it declined (Fig. 7).

Throughout most of the study the Typha stand was located 0.5-1.0 m from the shoreline; however, this distance varied up to a maximum of approximately 40 m in spring and summer 1974 due to the fluctuating water level.

The variation in water temperature in the Typha stand is shown in Fig. 8. The first measurement was taken on May 8, 1973, approximately one and a half weeks after the ice melted, when a value of 12°C was recorded. Thereafter the temperature increased, though fluctuating strongly, until July 31, when a maximum of 30.5°C was

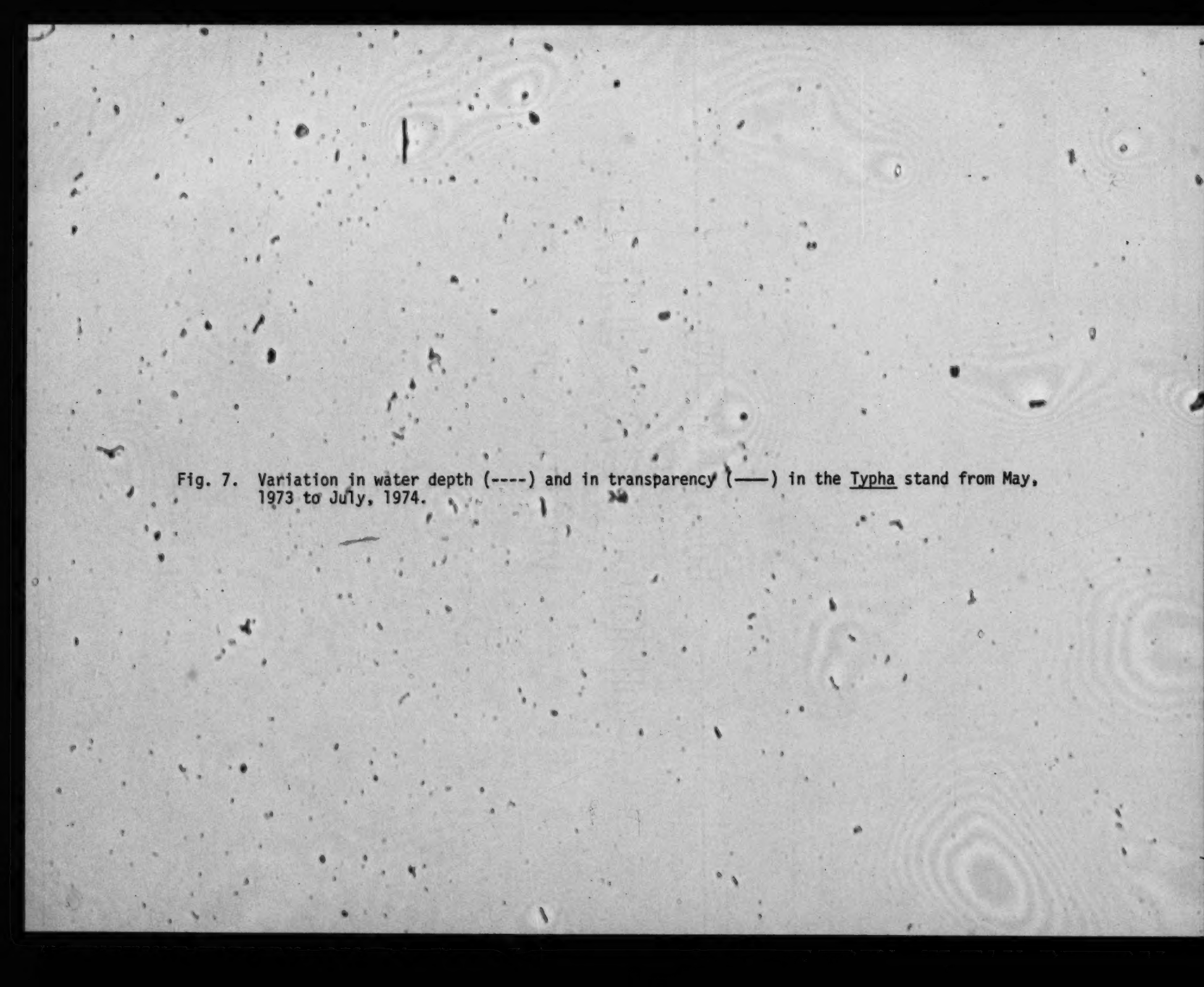
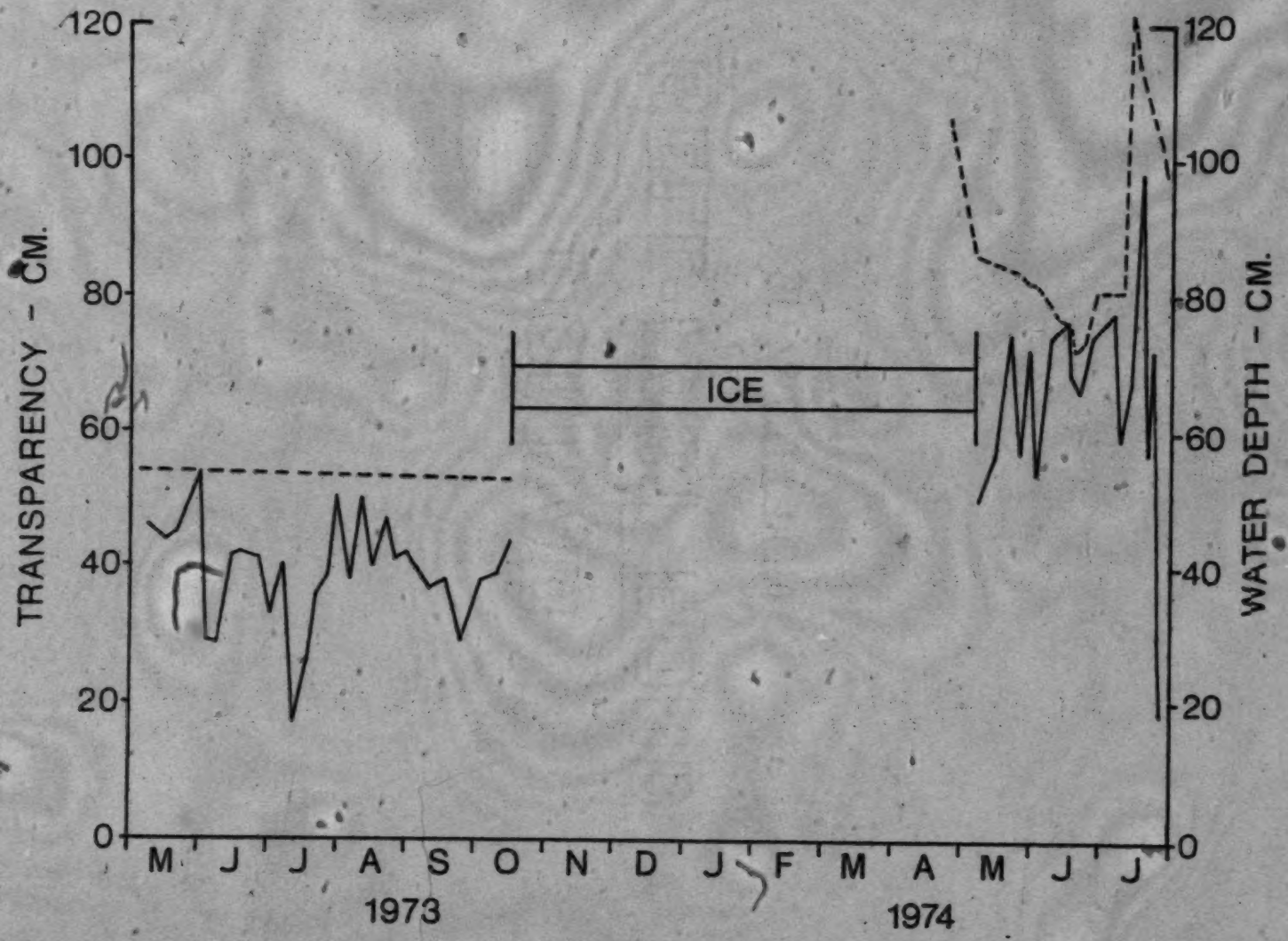


Fig. 7. Variation in water depth (----) and in transparency (——) in the Typha stand from May, 1973 to July, 1974.


120
100
80
60
40
20
0
TRANSPARENCY - CM.
WATER DEPTH - CM.
ICE
M J J A S O N D J F M A M J J
1973
1974

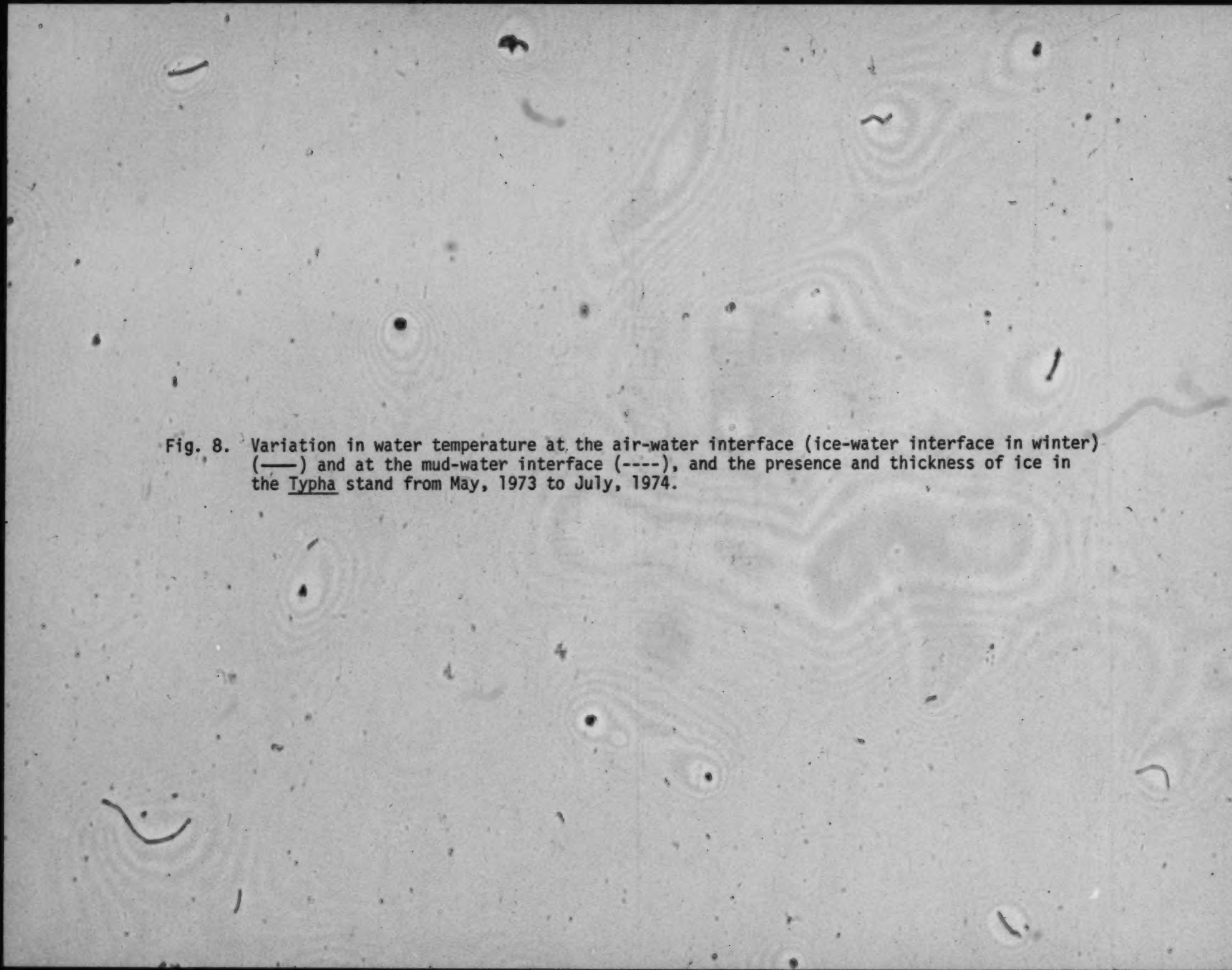
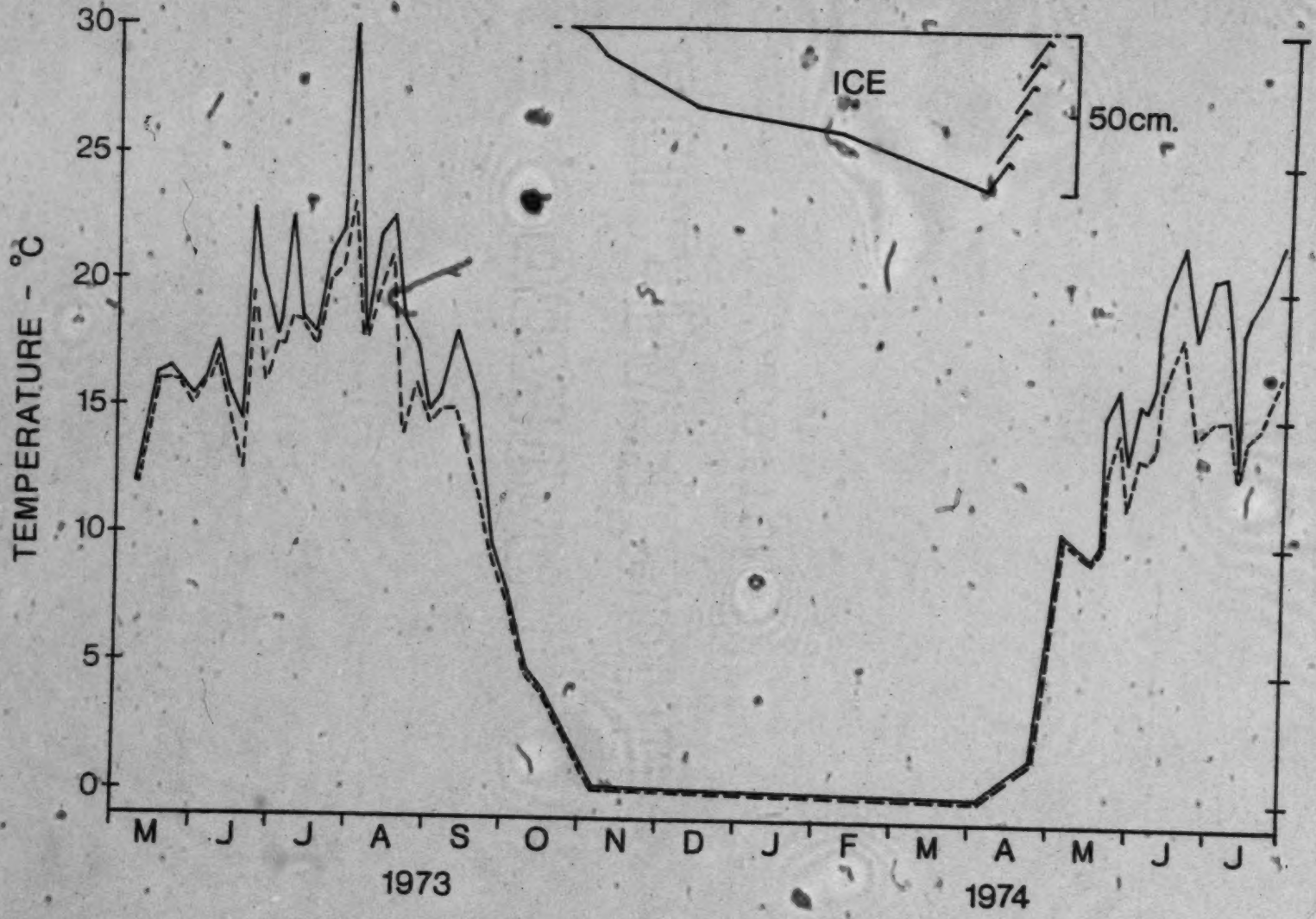


Fig. 8. Variation in water temperature at the air-water interface (ice-water interface in winter) (——) and at the mud-water interface (----), and the presence and thickness of ice in the Typha stand from May, 1973 to July, 1974.


30
25
20
15
10
5
0
TEMPERATURE - °C
ICE
50cm.
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
1973
1974

recorded at the air-water interface. Subsequently, the temperature dropped sharply to 18°C on August 5. The maximum temperature recorded in August was 22.5°C on the 15th., and in September was 18°C on the 10th. By October 15 it had dropped to 4°C, and by November 5 it was 0°C.

Ice was recorded first on October 15 and increased in thickness as shown in Fig. 8. A maximum thickness of 51 cm was recorded on April 3, 1974, when it extended to the mud-water interface. Ice was still present in the study area on April 25, but was covered with a layer of water approximately 60 cm deep. On May 4 all the ice had disappeared, and the water was isothermal at 11°C. Thereafter the temperature increased, though fluctuating, to a maximum of 23°C on June 22. A value of 13°C was recorded on July 13. Subsequently, the water temperature increased to 22°C on July 27. No measurements were made after July 30.

At no time during either summer was there any evidence of thermal stratification in the study area.

Changes in water transparency in the Typha stand are shown in Fig. 7. Only on two occasions, May 30, 1973, and June 15, 1974, could the Secchi disc be seen at the mud-water interface.

C. Efficiency of Emergence Trap.

1. Trapping Efficiency.

Results showing the number of chironomid adults of all species collected within the polythene tent and in each of the six emergence traps during each of the 10 collection periods are given in Table 1.

Table 1. Number of chironomid adults collected within the polythene tent and in each of the six emergence traps (T_1 - T_6) during the 10 collection periods.

Collection Period	Number in Tent	Number in Emergence Traps						Total Number Emerged
		T_1	T_2	T_3	T_4	T_5	T_6	
A	158	3	0	4	2	0	4	171
B	228	4	5	3	6	4	6	256
C	420	7	21	10	10	13	12	493
D	517	8	17	6	8	18	15	589
E	525	8	23	12	12	26	17	623
F	374	9	12	4	7	14	7	427
G	207	6	9	5	6	6	4	243
H	150	1	2	0	0	2	2	157
I	119	5	2	0	0	5	1	132
J	97	1	0	3	2	3	2	108

As the calendar dates are irrelevant, each of the original collection periods has been assigned a letter (A-J).

A paired t-test was performed to determine if there was a significant difference ($P \leq 0.05$) between the number of adults caught in the peripheral traps (T_1, T_2, T_3) and in the central traps (T_4, T_5, T_6). Results indicated that there was no significant difference (Table 2).

As there was no edge effect, the data from all six traps were combined to determine if the trapping efficiency of the emergence trap for all species of chironomids combined differed significantly from 100%. Since the six emergence traps sampled an area of 0.6 m^2 the number of specimens collected in the polythene tent, i.e. emerging outside the six emergence traps, was expressed in the same units, and a paired t-test performed using the pairs of values obtained on all sampling dates (Table 3). Results indicated that the efficiency of the trap did not differ significantly from 100%.

Identical analyses were performed on the data for each of the three most abundant species. These showed that there was no edge effect for any of the three species (Tables 4, 6 and 8) and that the efficiency of the trap for capturing G. lobiferus and D. nervosus did not differ significantly from 100% (Tables 5 and 9); however, for Endochironomus n. sp. the deviation in efficiency was significant, but just barely so (Table 7).

2. Retention Efficiency.

a) Addition of a constant number of specimens each day. Results obtained from these experiments are given in Table 10. The

Table 2. t-test to determine if there was a significant difference between the number of chironomids of all species caught in the peripheral ($T_1+T_2+T_3$) and in the central ($T_4+T_5+T_6$) emergence traps.

Collection Period	Number in Peripheral Traps	log # in Peripheral Traps	Number in Central Traps	log # in Central Traps
A	7	0.8451	6	0.7782
B	12	1.0792	16	1.2041
C	38	1.5798	35	1.5441
D	31	1.4914	41	1.6128
E	43	1.6335	55	1.7404
F	25	1.3979	28	1.4472
G	20	1.3010	16	1.2041
H	3	0.4771	4	0.6021
I	7	0.8451	6	0.7782
J	4	0.6021	7	0.8451

t for 9 DF at $P \leq 0.05 = 2.26$ Calculated t = 1.42

Table 3. t-test to determine if the trapping efficiency of the emergence trap for all species of chironomids combined was significantly different from 100%.

Collection Period	Number Emerging per 0.6 m^2			
	Inside the Traps		Outside the Traps	
	x	log x	y	log y
A	13	1.1139	24.2	1.3838
B	28	1.4472	34.9	1.5428
C	73	1.8633	64.3	1.8082
D	72	1.8573	79.1	1.8982
E	98	1.9912	80.3	1.9047
F	53	1.7243	57.2	1.7574
G	36	1.5563	31.7	1.5011
H	7	0.8451	23.0	1.3617
I	13	1.1139	18.2	1.2601
J	11	1.0414	14.8	1.1703

t for 9 DF at $P \leq 0.05 = 2.26$ Calculated t = 1.80

Table 4. t-test to determine if there was a significant difference between the number of G. lobiferus caught in the peripheral ($T_1+T_2+T_3$) and in the central ($T_4+T_5+T_6$) emergence traps.

Collection Period	Number in Peripheral Traps	log # in Peripheral Traps	Number in Central Traps	log # in Central Traps
A	3	0.4771	2	0.3010
B	5	0.6990	6	0.7782
C	15	1.1761	9	0.9542
D	12	1.0792	7	0.8451
E	27	1.4314	40	1.6021
F	16	1.2041	24	1.3802
G	16	1.2041	10	1.0000
H	3	0.4771	2	0.3010
I	7	0.8451	5	0.6990
J	2	0.3010	7	0.8451

t for 9 DF at $P \leq 0.05 = 2.26$ Calculated t = 0.23

Table 5. t-test to determine if the trapping efficiency of the emergence trap for G. lobiferus was significantly different from 100%.

Collection Period	Number Emerging per 0.6 m^2			
	Inside the Traps		Outside the Traps	
	x	log x	y	log y
A	5	0.6990	12.5	1.0969
B	11	1.0414	12.1	1.0828
C	24	1.3802	18.7	1.2718
D	19	1.2788	27.4	1.4378
E	67	1.8261	46.7	1.6693
F	40	1.6021	39.9	1.6010
G	26	1.4150	24.5	1.3892
H	5	0.6990	18.8	1.2742
I	12	1.0792	15.9	1.2014
J	9	0.9542	12.5	1.0969
t for 9 DF at $P \leq 0.05 = 2.26$			Calculated t = 1.61	

Table 6. t-test to determine if there was a significant difference between the number of Endochironomus n. sp. caught in the peripheral ($T_1+T_2+T_3$) and in the central ($T_4+T_5+T_6$) emergence traps.

Collection Period	Number in Peripheral Traps	log # in Peripheral Traps	Number in Central Traps	log # in Central Traps
A+B	2	0.3010	5	0.6990
C	18	1.2553	16	1.2041
D	13	1.1139	29	1.4624
E	14	1.1461	15	1.1761
F	8	0.9031	4	0.6021
G	3	0.4771	4	0.6021
H+I+J	1	0.0000	3	0.4771

t for 6 DF at $P \leq 0.05 = 2.45$ Calculated t = 1.38

Table 7. t-test to determine if the trapping efficiency of the emergence trap for Endochironomus n. sp. was significantly different from 100%.

Collection Period	Number Emerging per 0.6 m^2			
	Inside the Traps		Outside the Traps	
	x	log x	y	log y
A+B	7	0.8451	13.8	1.1399
C	34	1.5315	34.9	1.5428
D	42	1.6232	46.2	1.6646
E	29	1.4624	32.0	1.5051
F	12	1.0792	16.8	1.2253
G	7	0.8451	6.9	0.8388
H+I+J	4	0.6021	7.0	0.8451
t for 6 DF at $P \leq 0.05$ = 2.447			Calculated t = 2.453	

Table 8. t-test to determine if there was a significant difference between the number of D. nervosus caught in the peripheral ($T_1+T_2+T_3$) and in the central ($T_4+T_5+T_6$) emergence traps.

Collection Period	Number in Peripheral Traps	log # in Peripheral Traps	Number in Central Traps	log # in Central Traps
A	1	0.0000	3	0.4771
B	2	0.3010	4	0.6021
C	4	0.6021	9	0.9542
D - J	9	0.9542	5	0.6990

t for 3 DF at $P \leq 0.05 = 3.18$ Calculated t = 1.35

Table 9. t-test to determine if the trapping efficiency of the emergence trap for D. nervosus was significantly different from 100%.

Collection Period	Number Emerging per 0.6 m^2			
	Inside the Traps		Outside the Traps	
	x	log x	y	log y
A	4	0.6021	6.6	0.8195
B	6	0.7782	8.9	0.9494
C	13	1.1139	9.8	0.9912
D	10	1.0000	4.9	0.6902
E	2	0.3010	1.5	0.1761
F - J	2	0.3010	2.0	0.3010

t for 5 DF at $P \leq 0.05 = 2.57$ Calculated t = 0.35

Table 10. Results from experiments to determine the retention efficiency of the emergence trap based on addition of a constant number of specimens each day.

Starting No. and No. added each day	No. of days after starting expt.							Cumulative number lost			
	1	2	3	4	5	6	7	After four days		After seven days	
	Cumulative number retained							M	F	M	F
2	2	4	6	8	8	9	10	0	0	1	3
2	2	4	6	6	7	8	9	1	1	2	3
2	2	4	6	7	7	8	8	0	1	2	4
2	2	4	4	6	8	10	12	0	2	0	2
2	2	3	5	7	9	10	12	0	1	1	1
4	4	8	12	15	18	22	26	0	1	0	2
4	4	8	12	14	17	20	23	1	1	2	3
4	3	7	10	14	17	21	24	1	1	2	2
4	4	8	9	12	13	15	19	1	3	3	6
6	6	11	14	16	15	21	23	3	5	7	12
6	6	11	14	14	16	22	24	7	3	11	7
6	6	12	16	22	28	33	38	1	1	2	2
6	5	10	14	19	23	28	33	2	3	3	6
8	8	16	21	25	28	31	30	5	2	15	11
8	6	13	21	23	28	32	36	3	6	8	12
8	6	14	19	27	34	42	48	2	3	5	3
8	8	16	20	25	29	34	39	3	4	7	10
8	8	12	16	21	27	32	37	4	7	7	12
10	10	19	26	32	36	39	41	3	5	13	16
10	9	18	24	28	33	40	47	5	7	9	14

data were analyzed to determine if a significant correlation existed between the percentage retention and the number of adults placed in the trap, i.e. if the retention efficiency was density-dependent, both variables being cumulative. The correlation coefficient was determined for each of the seven days of experimentation but none was significant ($P < 0.05$). Consequently, the data from all experiments were combined and a correlation coefficient calculated between the cumulative percentage retention and the number of days expired since commencement of the experiment, i.e. the number of days since last emptying the traps. A correlation coefficient of 0.618 was obtained which is significant at $P < 0.005$. The correlation coefficients for the semi-logarithmic and the log-log relationship were checked also, and values of 0.612 and 0.310 respectively were obtained. The best-fit regression line is given by the equation $Y = 11.44 - 0.09X$ (Fig. 9).

Application of a Chi-Squared test to the sex ratio of the cumulative number of adults lost after four and after seven days (Table 10), using the number of males and of females as the observed values and the mean of the total number of adults of both sexes combined as the expected values, showed that the sex ratio did not deviate significantly ($P < 0.05$) from unity after four days (Table 11), but did so after seven days (Table 12).

b) Addition of all specimens at one specific time. Results obtained from these experiments are given in Table 13. Analyses of the data as outlined above showed that a significant correlation ($P < 0.05$) did not exist between the percentage retention and the

Fig. 9. Variation in percentage retention of adult G. lobiferus by the new emergence trap based on addition of a constant number of specimens to the trap each day. The regression equation is Y = 11.44 - 0.09X. The correlation coefficient is 0.618 and is significant at $P < 0.005$.

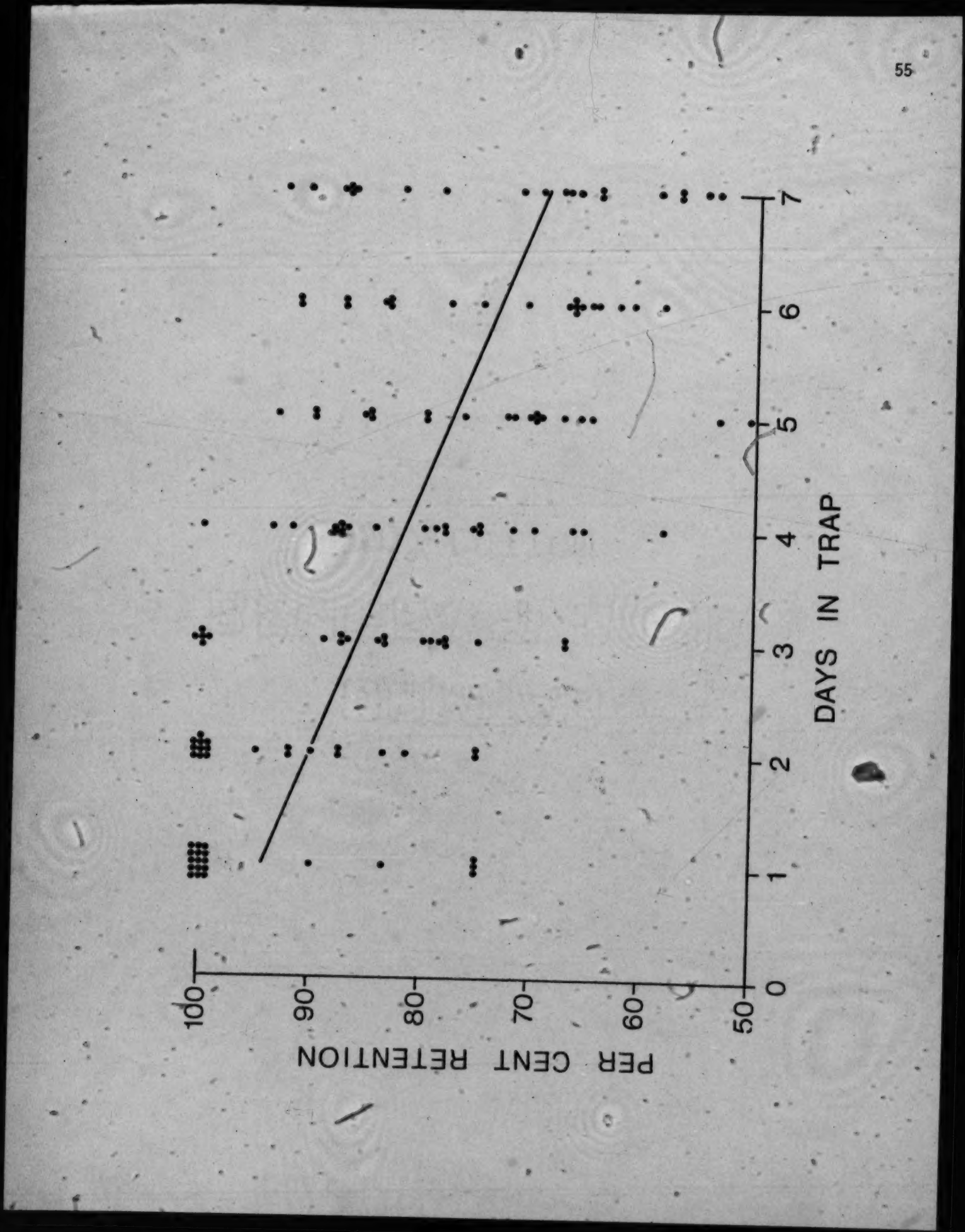

PER CENT RETENTION
100
90
80
70
60
50
0
1
2
3
4
5
6
7
DAYS IN TRAP

Table 11. Chi-Squared test to determine if any difference existed between the cumulative number of males and of females not retained by the emergence traps after four days. Data from Table 10.

	Observed	Expected	$\frac{(O-E)^2}{E}$
Males	42	49.5	1.14
Females	57	49.5	1.14
	99	99.0	2.28

X^2 for 1 DF at $P \leq 0.05 = 3.84$

Table 12. Chi-Squared test to determine if any difference existed between the cumulative number of males and of females not retained by the emergence traps after seven days. Data from Table 10.

	Observed	Expected	$\frac{(O-E)^2}{E}$
Males	100	115.5	2.08
Females	131	115.5	2.08
	231	231.0	4.16

X^2 for 1 DF at $P \leq 0.05 = 3.84$

Table 13. Results from experiments to determine the retention efficiency of the emergence trap based on addition of all specimens just at one specific time.

Number placed in trap	Number of days after starting experiment					Number lost	
	1	2	3	4	5		
	Cumulative number retained					M	F
2	2	2	2	2	2	0	0
4	4	4	2	2	2	1	1
6	6	6	5	5	5	0	1
6	6	6	5	4	4	0	2
8	7	7	6	5	5	1	2
8	5	4	4	3	3	2	3
10	10	10	10	10	10	0	0
10	9	8	8	8	7	1	2
10	9	7	7	7	7	0	3
14	14	14	14	13	12	1	1
16	16	16	15	15	15	1	0
16	14	13	10	10	10	2	4
18	17	17	16	15	15	1	2
20	20	18	15	15	15	1	4
22	22	20	17	17	17	2	3
22	21	16	13	13	11	4	7
28	27	25	19	18	18	4	6
32	31	29	20	18	16	7	9
34	33	30	26	25	25	4	5
34	34	33	32	32	30	3	1
44	38	35	29	27	24	7	13

number placed in the trap, i.e. the emergence rate. Calculation of the correlation coefficient between the cumulative percentage retention and the number of days since the specimens were placed in the traps, i.e. the number of days since last emptying the traps, gave values of 0.578, 0.568 and 0.558 for the arithmetic, semi-logarithmic ant the log-log relationship. The best-fit regression line is given by the equation $Y = 100.78 - 5.66X$ (Fig. 10).

Application of a Chi-Squared test to the sex ratio of the cumulative number of adults lost at the end of all experiments (Table 14), using the number of males and of females as the observed values and the mean of the total number of adults of both sexes combined as the expected values, showed that the sex ratio did deviate significantly ($P \leq 0.05$) from unity.

D. Fecundity of Chironomids.

In Appendix I, which deals with the morphological differentiation of G. dreisbachi, G. lobiferus and G. nr. paripes in all developmental stages, a table is given (Table 1) which includes data on the number of eggs per egg mass of each species. In summary, the mean number of eggs per egg mass in G. dreisbachi was 519.4, in G. lobiferus it was 1313.2, and in G. nr. paripes it was 1007.7. The value for G. dreisbachi is based solely on egg masses collected in the spring, whereas those for the other two species are based on egg masses collected in spring (=May) and summer (=June-September).

Comparison of the number of eggs in seven egg masses collected in spring and in six collected in summer showed no essential difference

60

Fig. 10. Variation in percentage retention of adult G. lobiferus by the new emergence trap based on addition of a known number of specimens just at one specific time. The regression equation is Y - 100.78 - 5.66X. The correlation coefficient is 0.578 and is significant at $P \leq 0.005$.

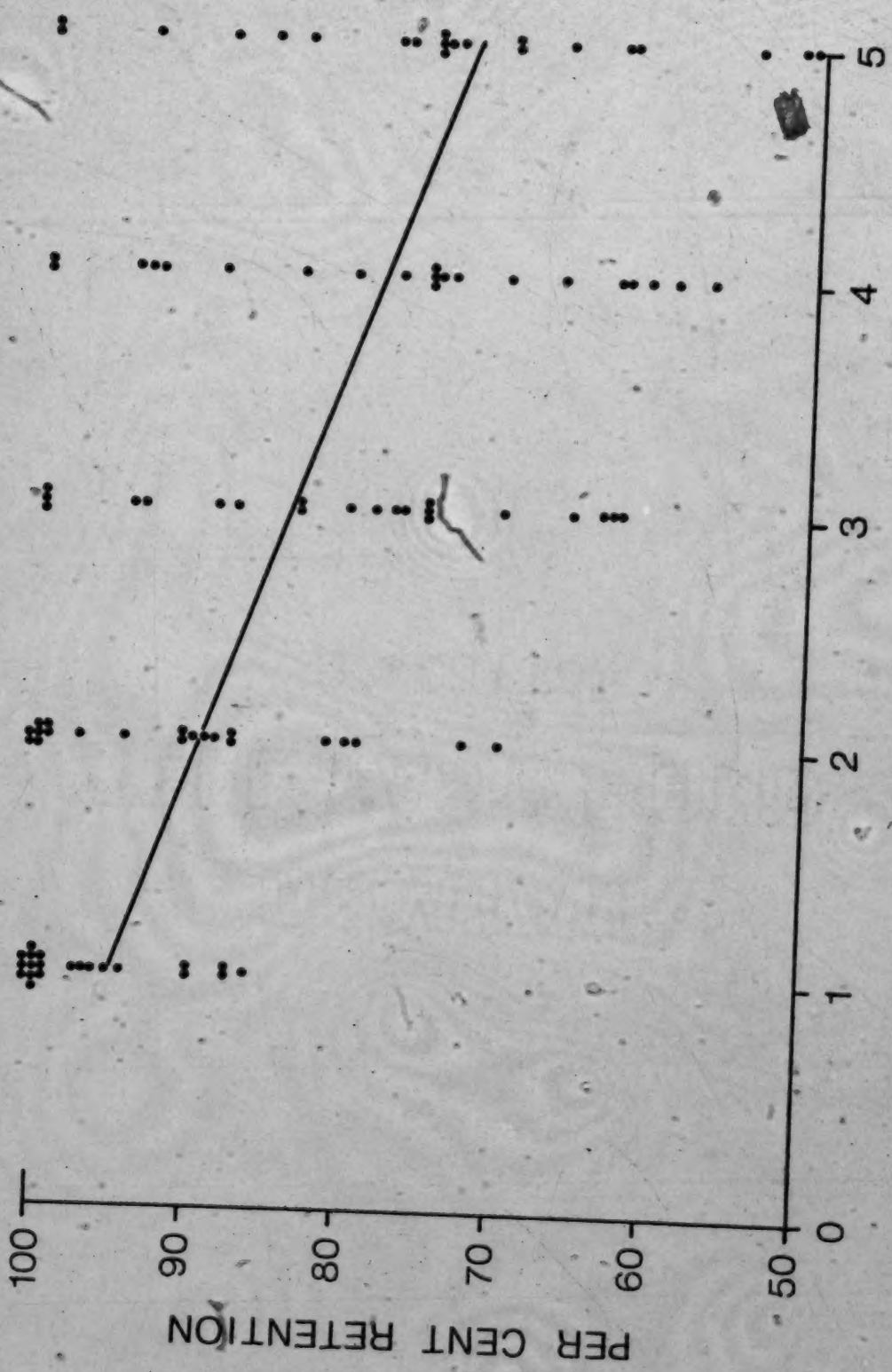

PER CENT RETENTION
100
90
80
70
60
50
0
1
2
3
4
5
DAYS IN TRAP

Table 14. Chi-Squared test to determine if any difference existed between the total number of males and of females not retained by the emergence traps. Data from Table 13.

	Observed	Expected	$\frac{(O-E)^2}{E}$
Males	42	55.5	3.28
Females	69	55.5	3.28
	111	111.0	6.56

X^2 for 1 DF at $P \leq 0.05 = 3.84$

for G. nr. paripes, viz. 1009.7 and 1005.3 eggs per egg mass respectively. Examination of five spring and 12 summer egg masses of G. lobiferus gave mean values of 1248.0 and 1340.3 respectively.

For D. nervosus, the number of eggs was determined in only three egg masses. One was collected on June 13, and two on July 1, 1973. They contained 362, 363 and 312 eggs respectively, giving a mean value of 345.7 eggs per egg mass.

E. Life Tables[4].

1. Dicrotendipes nervosus

Six egg masses were found in the egg traps between June 13 and July 1, 1973; all except one were collected between June 13 and 17. The mean number of eggs laid per square meter was 2880.0, and the 95% confidence limits were 1210.0 - 4667.0. Fifty per cent of the eggs were laid by June 15.

Plant and core samples were collected on June 17, but no first instar larvae were found until June 21, the subsequent sampling date. A plot of the density of the larvae of the new cohort in the live and the dead Typha shoots and on the lake bottom, and of their total density on each sampling date is given in Fig. 11 (all density estimates with their 95% confidence limits are tabulated in Appendix III). As indicated, larvae were collected in all three sub-habitats, but least frequently on the lake bottom, where none was found after October 1. A plot of the change in the per cent of the larvae in each instar is given

[4]For explanation of the symbols used and the equations used to derive the population statistics see Appendix II.

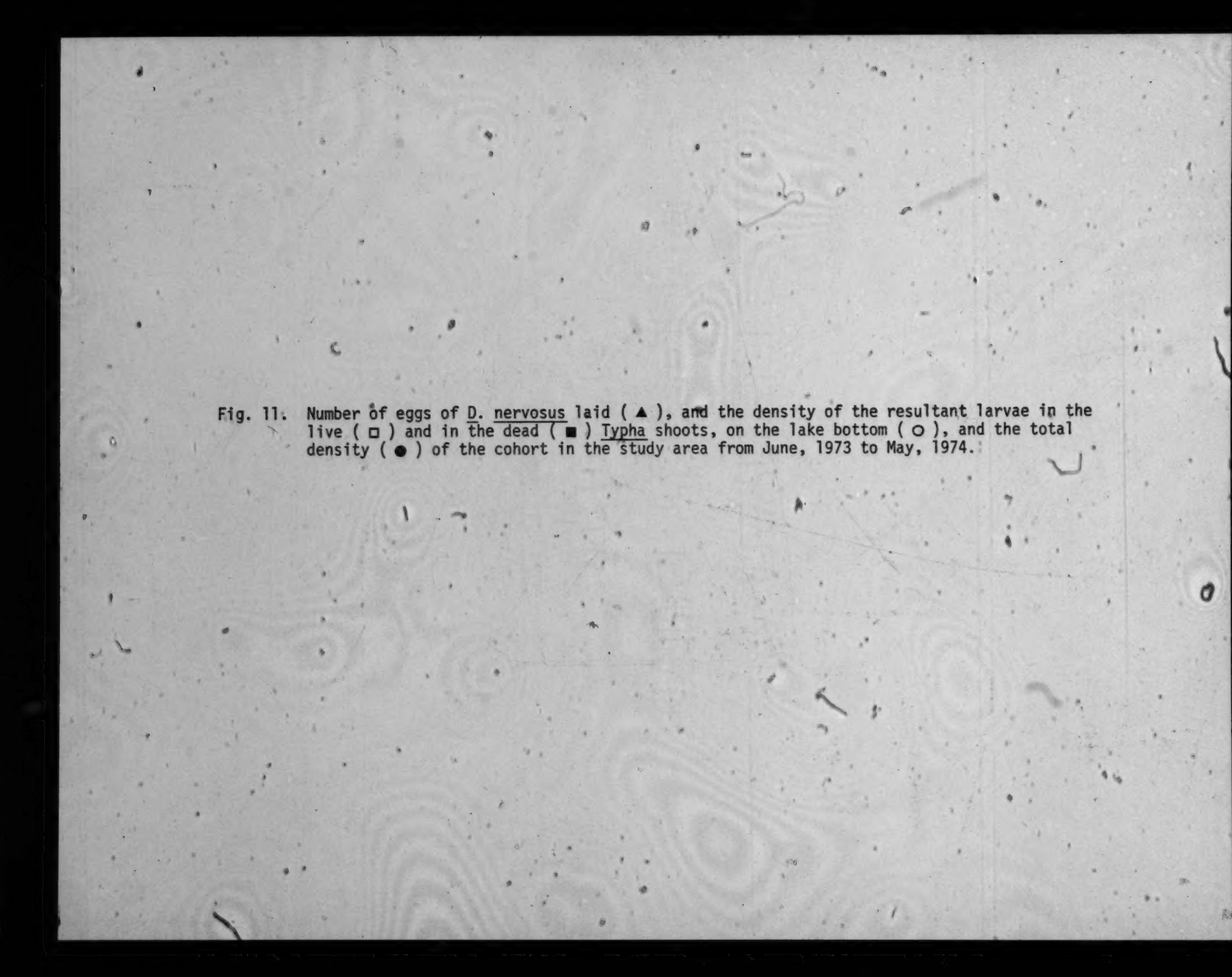
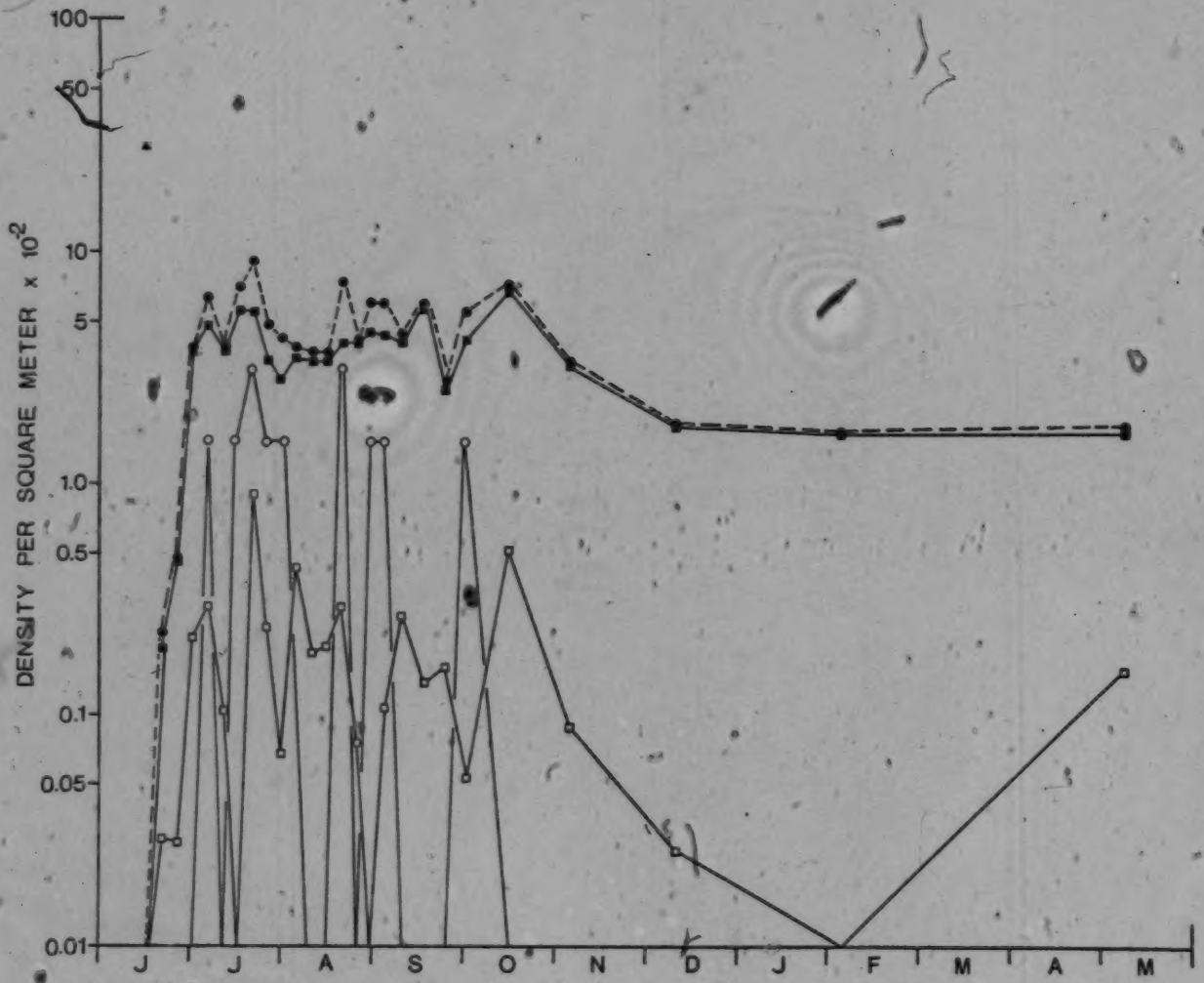


Fig. 11. Number of eggs of D. nervosus laid (▲), and the density of the resultant larvae in the live (□) and in the dead (■) Typha shoots, on the lake bottom (○), and the total density (●) of the cohort in the study area from June, 1973 to May, 1974.


100
50
10
5
1.0
0.5
0.1
0.05
0.01
DENSITY PER SQUARE METER x 10^{-2}
J
J
A
S
O
N
D
J
F
M
A
M

in Fig. 12.

Although the variance of the estimates of total larval density was high (Fig. 13D) a significant decrease did occur in population density, since calculation of the correlation coefficient between total larval density and time, starting with the peak density (920.6/m^2 - July 21), gave a value of 0.59 which is significant at $P < 0.05$.

Except for one female collected in an emergence trap on July 23, 1973, all adults were trapped between June 4 and July 14, 1974 (Fig. 14). A total of 62 adults were caught. Dates for completion of 25, 50 and 75% of emergence were June 13 and 17, and July 4 respectively. Estimates for the number of males, females and both sexes combined which successfully completed the aquatic phase of the life cycle (with the 95% confidence limits in parentheses) were 48.2 (22.6-81.4), 188.3 (121.8-267.3) and 236.5 (164.8-318.1) per square meter respectively.

A partial life table is given in Table 15, and various population statistics are given in Table 16.

2. Glyptotendipes dreisbachi

Eight egg masses of this species were found in the egg traps, and all were collected between May 22 and 25. The mean number of eggs laid per square meter was 6923.6, and the 95% confidence limits were 2088.0 - 9245.3. Fifty per cent were laid by May 24.

Although plant and core samples were collected on May 30, no larvae were found until June 3, the subsequent date of sampling. A plot of the density of the larvae per square meter in the live and in the dead Typha shoots, and of their total density on each sampling

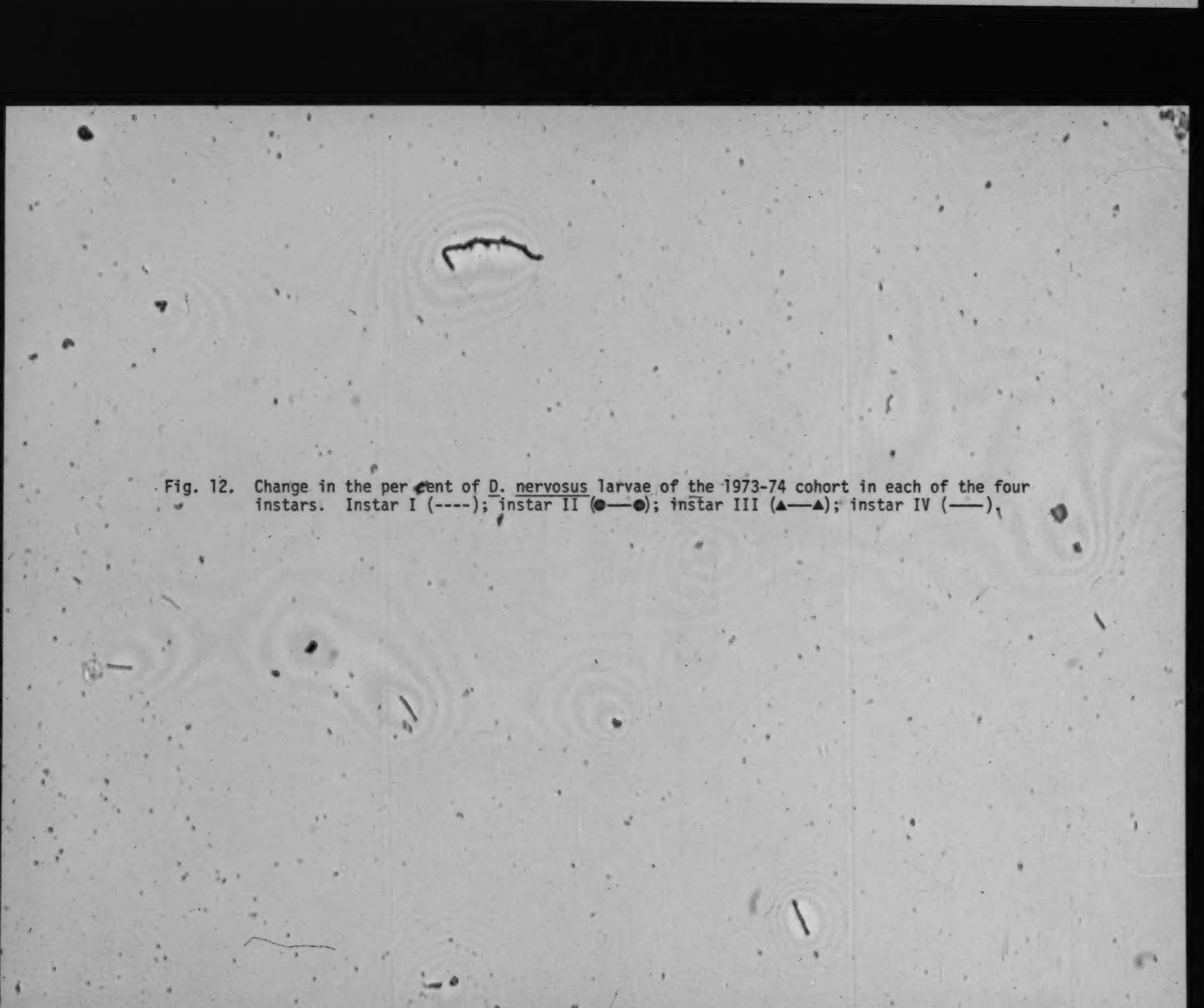
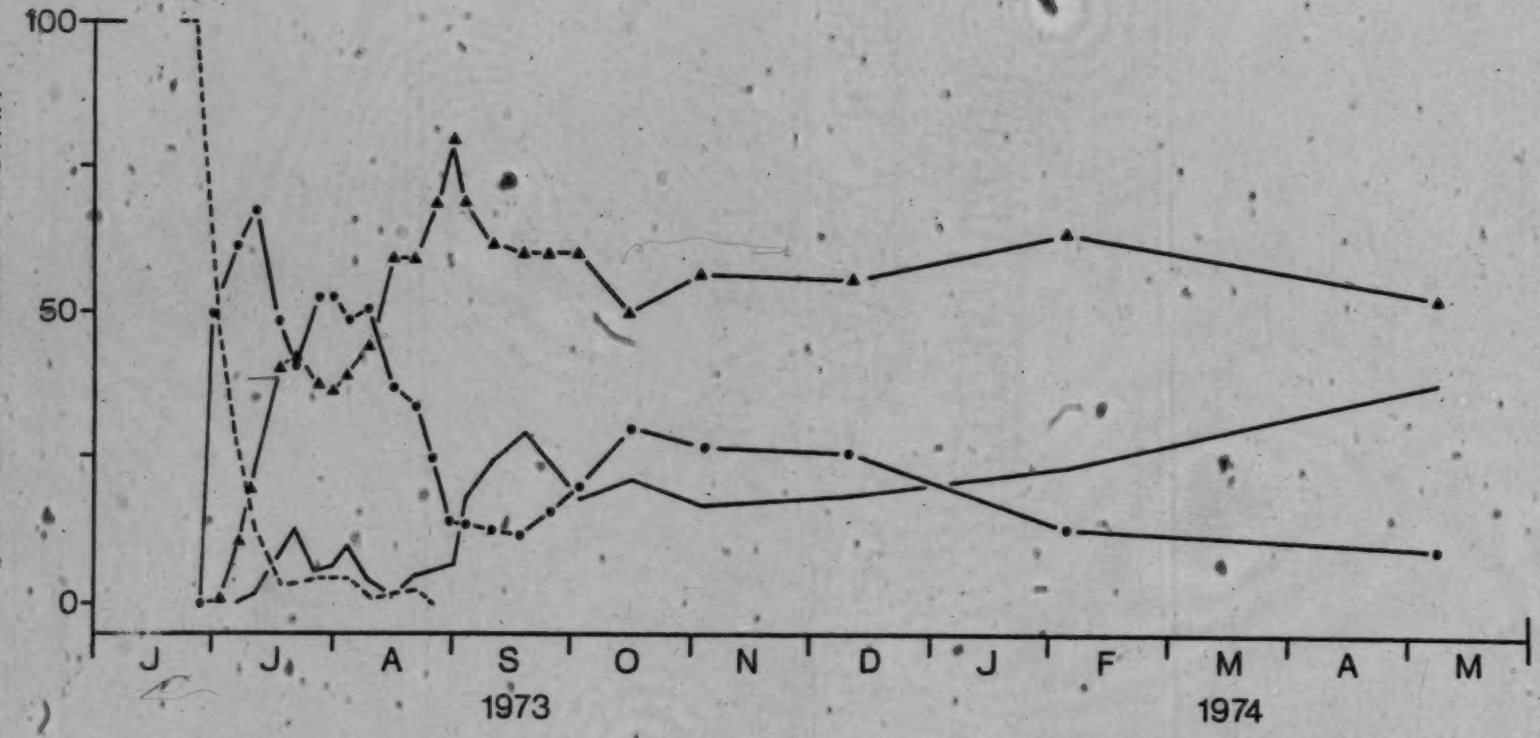


Fig. 12. Change in the per cent of D. nervosus larvae of the 1973-74 cohort in each of the four instars. Instar I (----); instar II (●—●); instar III (▲—▲); instar IV (——).


PER CENT IN EACH INSTAR
100
50
0
J
J
A
S
O
N
D
J
F
M
A
M
1973
1974

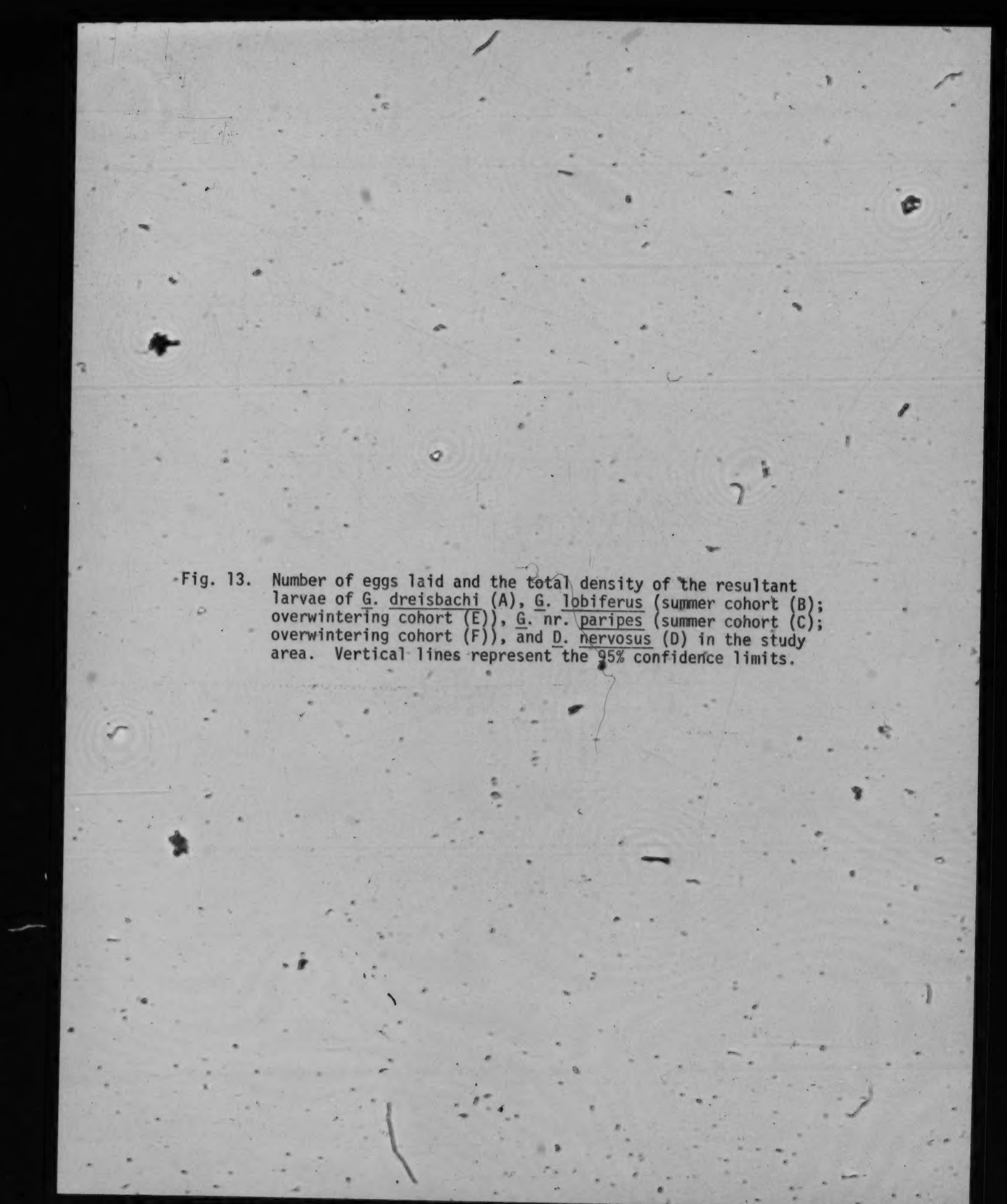
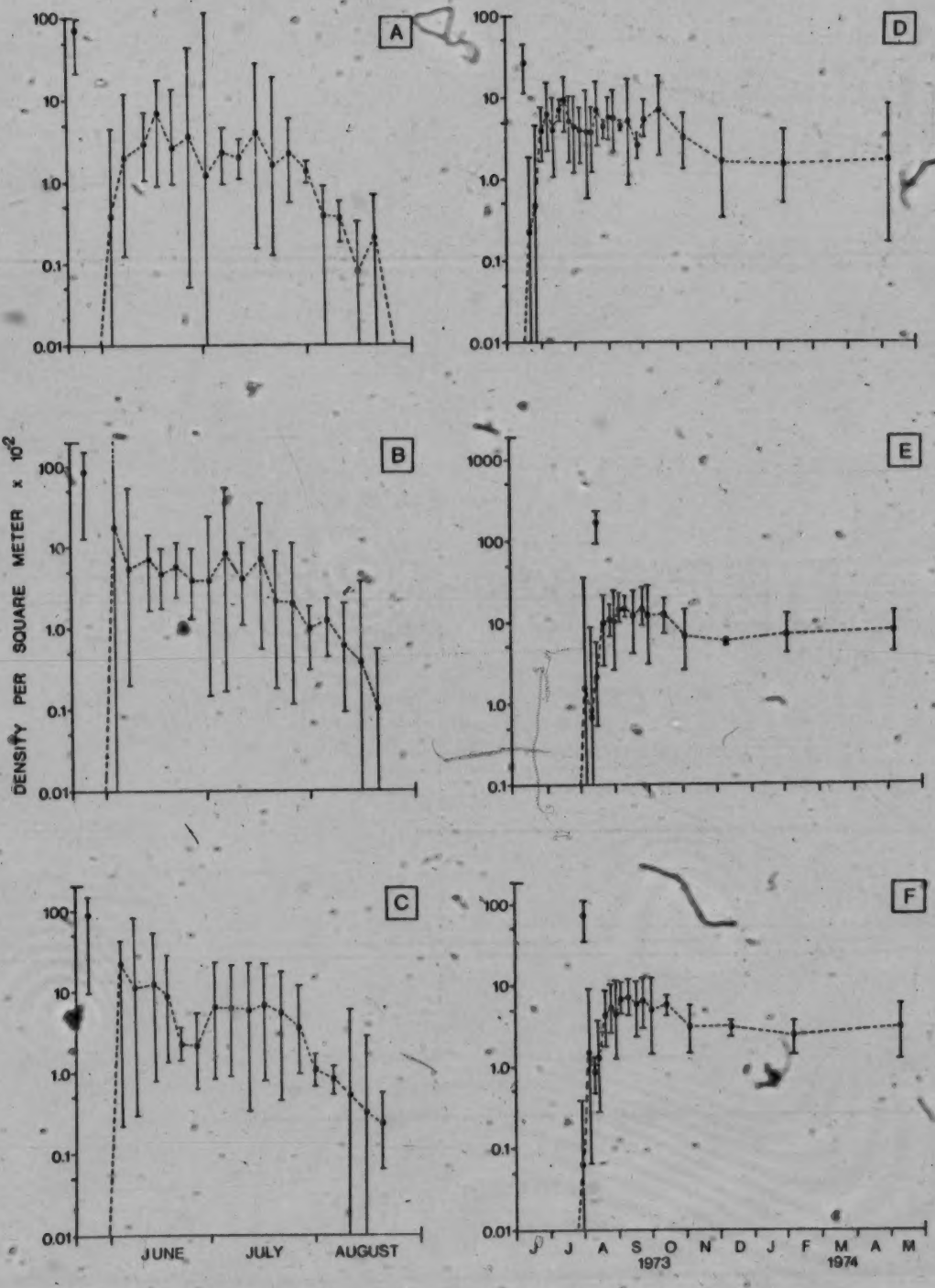


Fig. 13. Number of eggs laid and the total density of the resultant larvae of G. dreisbachi (A), G. lobiferus (summer cohort (B); overwintering cohort (E)), G. nr. paripes (summer cohort (C); overwintering cohort (F)), and D. nervosus (D) in the study area. Vertical lines represent the 95% confidence limits.


A
B
C
D
E
F
DENSITY PER SQUARE METER x 10^2
100
10
1.0
0.1
0.01
1000
JUNE
JULY
AUGUST
J J A S O N D J F M A M
1973
1974

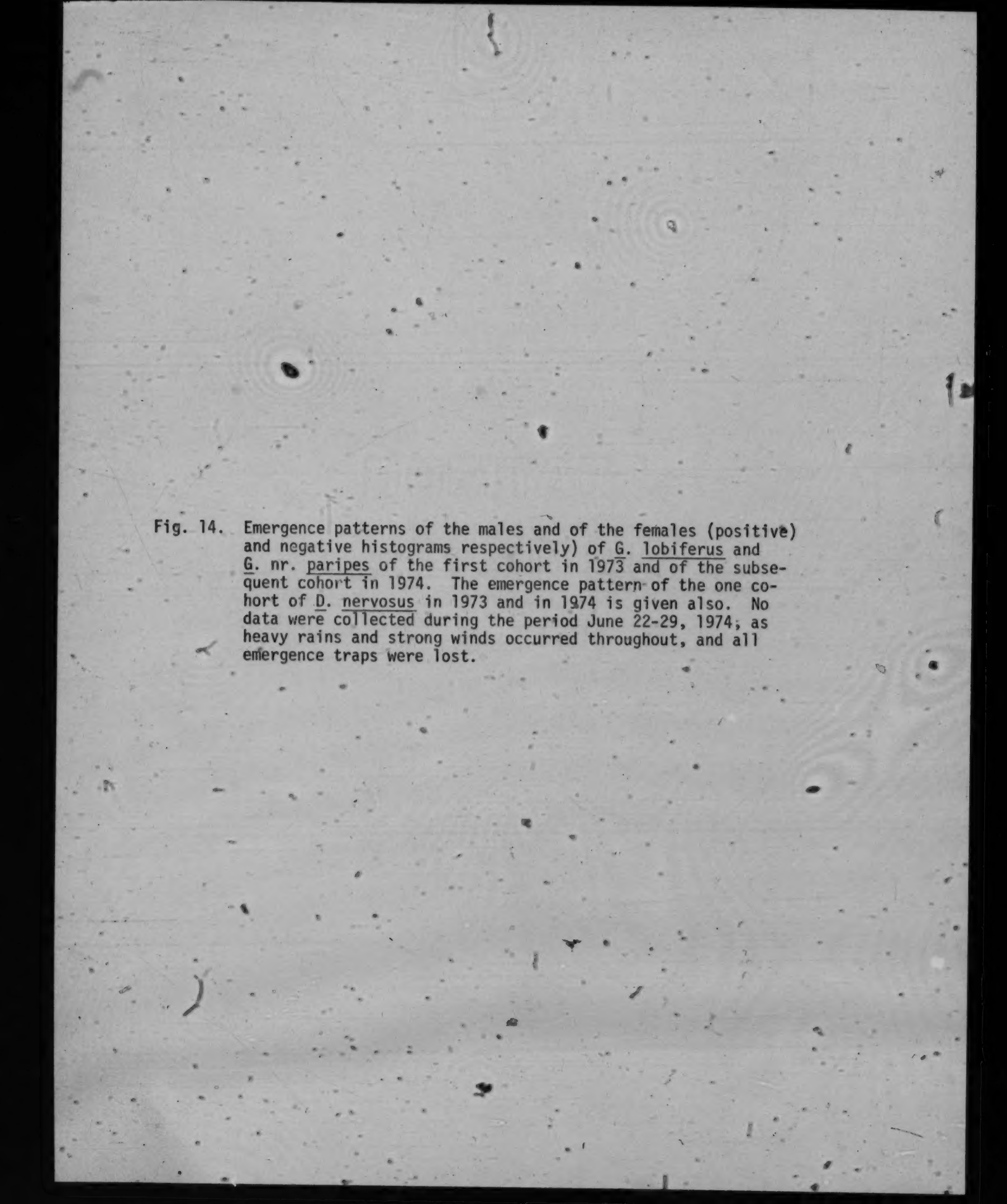


Fig. 14. Emergence patterns of the males and of the females (positive) and negative histograms respectively) of G. lobiferus and G. nr. paripes of the first cohort in 1973 and of the subsequent cohort in 1974. The emergence pattern of the one cohort of D. nervosus in 1973 and in 1974 is given also. No data were collected during the period June 22-29, 1974, as heavy rains and strong winds occurred throughout, and all emergence traps were lost.

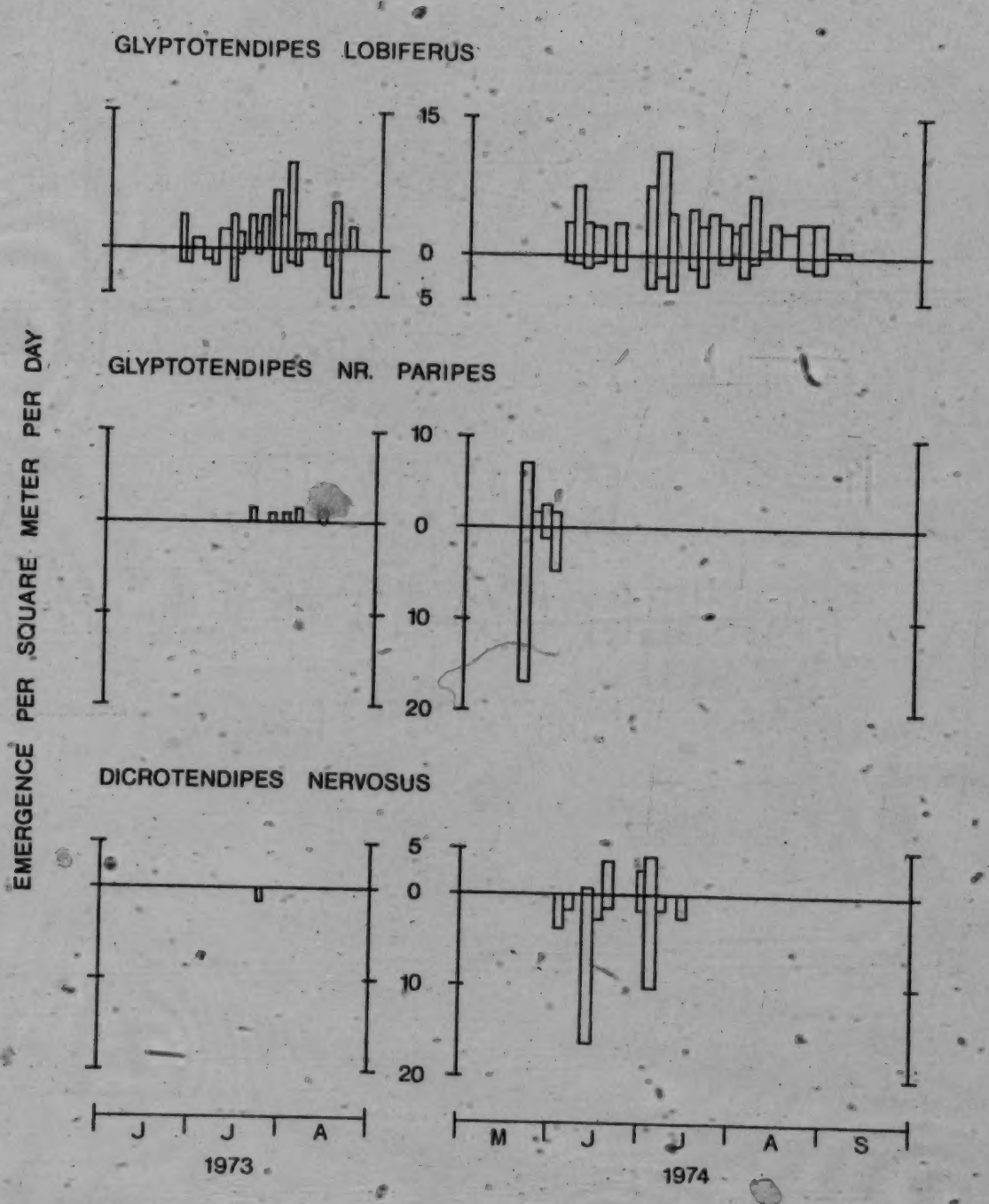

GLYPTOTENDIPES LOBIFERUS
15
0
5
GLYPTOTENDIPES NR. PARIPES
10
0
10
20
DICROTENDIPES NERVOSUS
5
0
10
20
EMERGENCE PER SQUARE METER PER DAY
J
J
A
1973
M
J
J
A
S
1974

TABLE 15. Partial life table for D. nervosus for its 1973-74 cohort. All densities expressed as number per square meter.

Sampling Date	Calendar Age (days)	% Duration of Cohort Completed	Larval Density	Adult Density M	Adult Density F	Total Population Density	Per Cent Population Surviving	Pivotal Age x (days)	No. of Females Surviving to Reproduce	l_x	V_x
June 15	0	0.0	2580.0			2580.0	100.0				
21	6	1.5	22.3			22.3		3.0			
26	11	2.8	48.4			48.4		8.5			
July 1	16	4.0	391.2			391.2		13.5			
6	21	5.3	667.9			667.9		18.5			
11	26	6.5	382.3			382.3		23.5			
16	31	7.8	713.1			713.1		28.5			
21	36	9.0	920.6			920.6	32.0	33.5			
26	41	10.3	518.8	0.0	2.356	521.2	18.1	38.5			
31	46	11.5	444.6			444.6	15.4	43.5	3.027	0.002	0.346
Aug. 5	51	12.8	385.4			385.4	13.4	48.5			
10	56	14.0	353.0			353.0	12.2	53.5			
15	61	15.3	355.0			355.0	12.3	58.5			
20	66	16.6	745.0			745.0	25.9	63.5			
25	71	17.8	411.2			411.2	14.3	68.5			
30	76	19.1	607.4			607.4	21.1	73.5			
Sept. 4	81	20.3	606.5			606.5	21.1	78.5			
10	87	21.8	451.0			451.0	15.6	84.0			
17	94	23.6	530.4			530.4	18.4	90.5			
24	101	25.4	268.3			268.3	9.3	97.9			
Oct. 1	108	27.1	582.0			582.0	20.2	104.5			
15	122	30.6	721.3			721.3	25.0	115.0			
Nov. 5	143	35.9	328.0			328.0	11.4	132.5			
Dec. 10	178	44.7	176.6			176.6	6.1	160.5			
Feb. 5	235	59.0	165.2			165.2	5.7	206.5			
May 8	327	82.1	180.3			180.3	6.3	281.5			
June 4	354	88.8		0.0	15.467			340.5			
6	356	89.3		0.0	9.843			355.0	12.655	0.009	1.555
10	360	90.3		0.0	0.000			358.0	0.000	0.000	0.000
13	363	91.1		4.1	85.500			361.5	0.000	0.000	0.000
17	367	92.1		1.1	34.918			365.0	69.954	0.048	8.294
20	370	92.8		16.3	13.406			368.5	9.491	0.006	1.037
25	375	94.1		1.5	8.739			372.5	6.654	0.005	0.854
30	380	95.4		11.6	7.733			377.5	0.000	0.000	0.000
July 4	384	96.4		19.3	42.809			382.0	6.327	0.004	0.691
8	388	97.4		4.4	18.833			386.0	33.300	0.023	3.974
11	391	98.1		0.0	3.515			389.5	6.327	0.004	0.691
14	394	98.9		0.0	7.733			392.5	0.000	0.000	0.000
17	397	99.6		0.0	3.515			395.5	6.327	0.004	0.691
20	399	100.0		0.0	0.000	0.0	0.0	398.5	0.000	0.000	0.000

Table 16. Comparison of population statistics for natural field populations of four species of chironomids.

Species	Cohort	Duration of Cohort (days)	T (days)	R_o	r_c	r_m	λ	Per Cent Survivorship Per Square Meter		
								Males	Females	Total
D. nervosus	Overwintering	398.5	370.4	17.80	0.0078	0.0077	1.008	3.35	13.08	8.21
G. dreisbachi	Summer	90.5	-	0.26	-	-	-	0.00	0.11	0.05
G. lobiferus	Summer	92.5	58.9	8.71	0.0367	0.0380	1.039	3.39	1.54	2.47
	Overwintering	394.0	331.3	9.67	0.0068	0.0067	1.007	5.44	1.63	3.53
G. nr. paripes	Summer	89.5	-	0.00	-	-	-	0.45	0.00	0.22
	Overwintering	312.0	300.3	13.63	0.0087	0.0087	1.009	1.57	3.29	2.43

date is given in Fig. 15 (all density estimates with their 95% confidence limits are tabulated in Appendix III). No larvae were found on the lake bottom. A plot of the change in the per cent of all larvae in each instar is given in Fig. 16A.

The variance of the estimates of total larval density was high (Fig. 13A); however, a significant decrease did occur in population density, since calculation of the correlation coefficient between total larval density and time, starting with the peak density (704.0 - June 17), gave a value of 0.78 which is significant at $P \leq 0.01$.

Only one adult, a female, was collected in the emergence traps, on August 7. This was equivalent to a survivorship of 3.7 per square meter. The 95% confidence limits were 0 - 23.6 per square meter.

A life table is given in Table 17, and various population statistics are given in Table 16.

3. Glyptotendipes lobiferus

a) First cohort. Four egg masses of the first cohort were found in the egg traps and all were collected during the period May 22-28. The mean number of eggs laid per square meter was 8324.2, and the 95% confidence limits were 1347.8 - 15475.2. Fifty per cent were laid by May 25.

Similar to G. dreisbachi, no first instar larvae were found until June 3. Larvae of G. lobiferus were found in all three sub-habitats, but least frequently in association with the live Typha shoots. A plot of the density of the larvae in the live and the dead Typha shoots and on the lake bottom, and of their total density on each sampling date is given in Fig. 17 (all density estimates with their

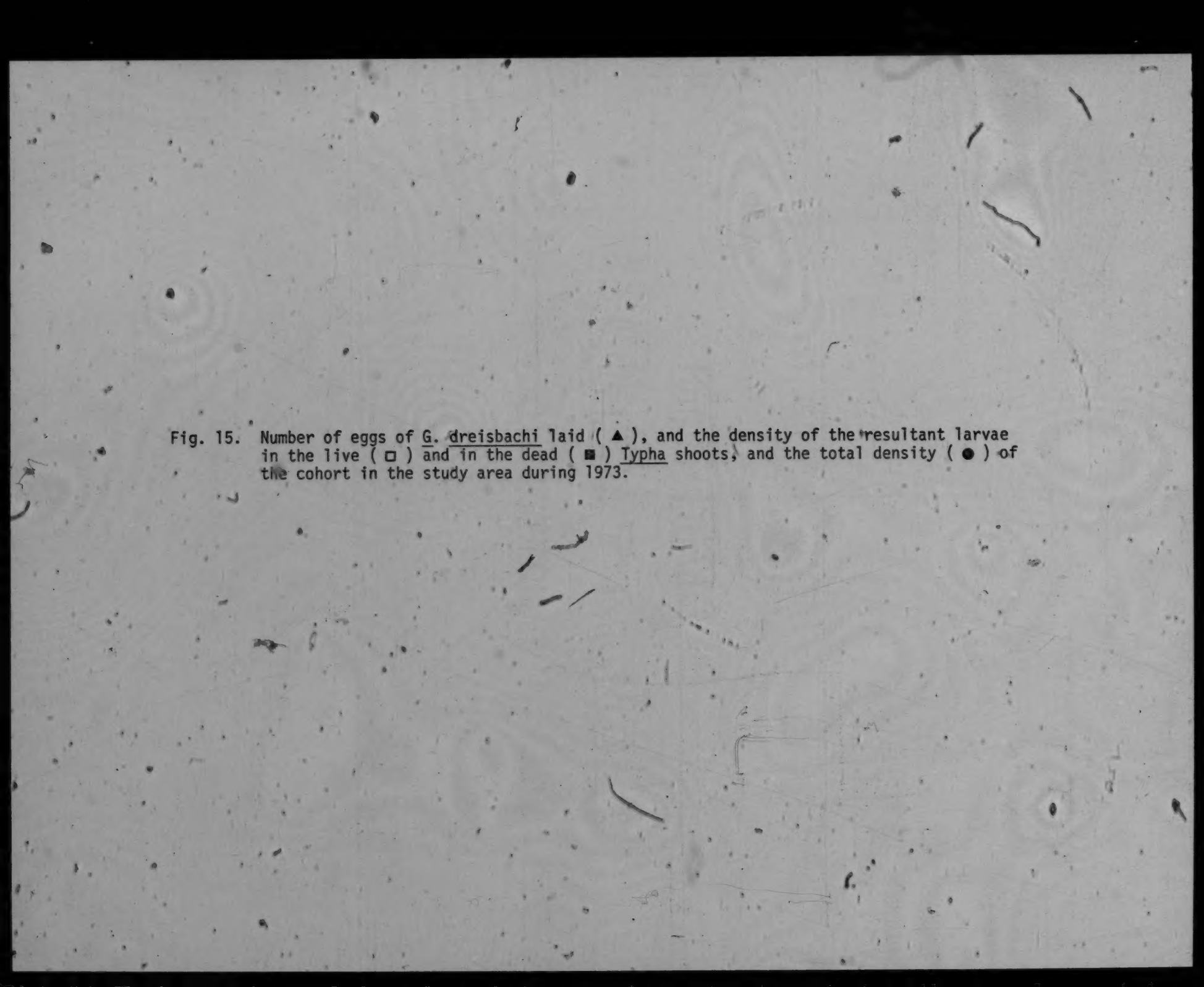
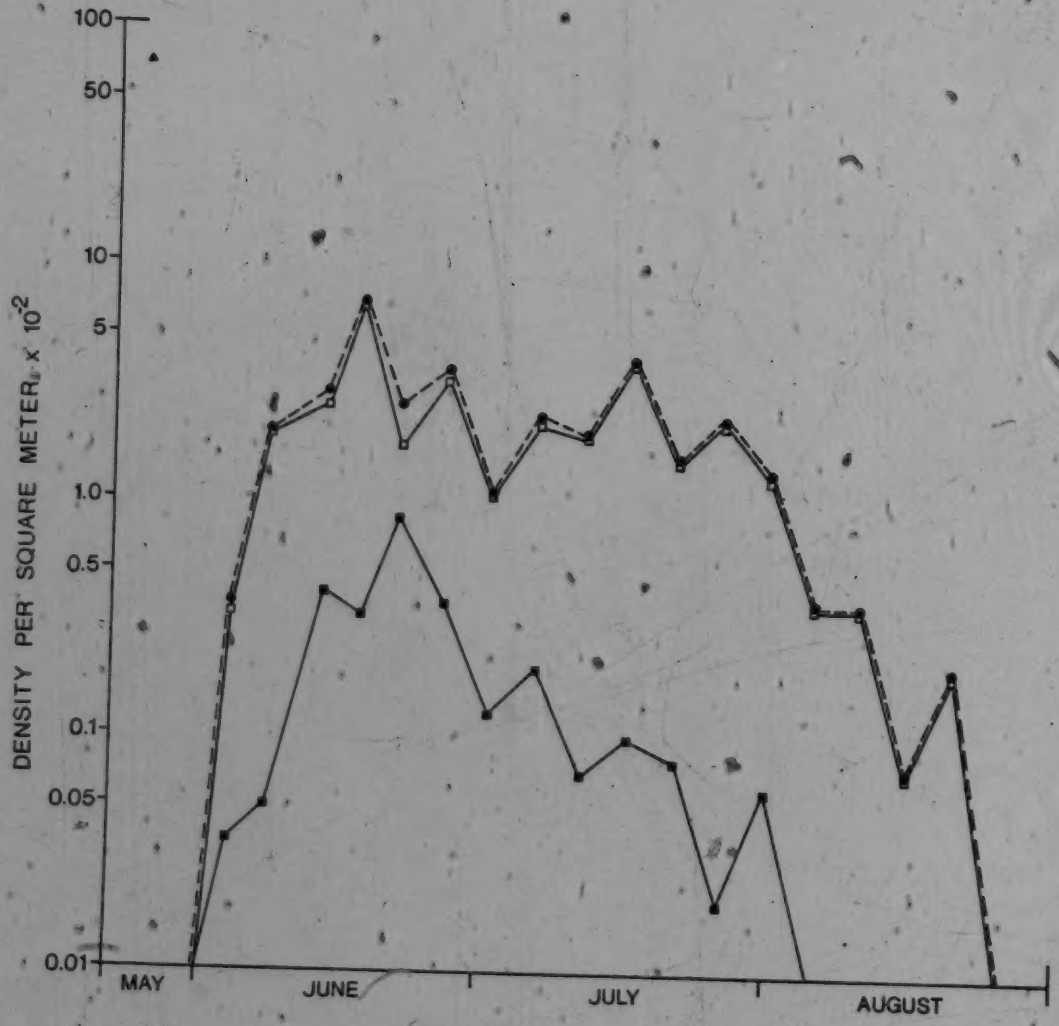


Fig. 15. Number of eggs of G. dreisbachi laid (▲), and the density of the resultant larvae in the live (□) and in the dead (■) Typha shoots, and the total density (●) of the cohort in the study area during 1973.


100
50
10
5
1.0
0.5
0.1
0.05
0.01
DENSITY PER SQUARE METER x 10^{-2}
MAY
JUNE
JULY
AUGUST

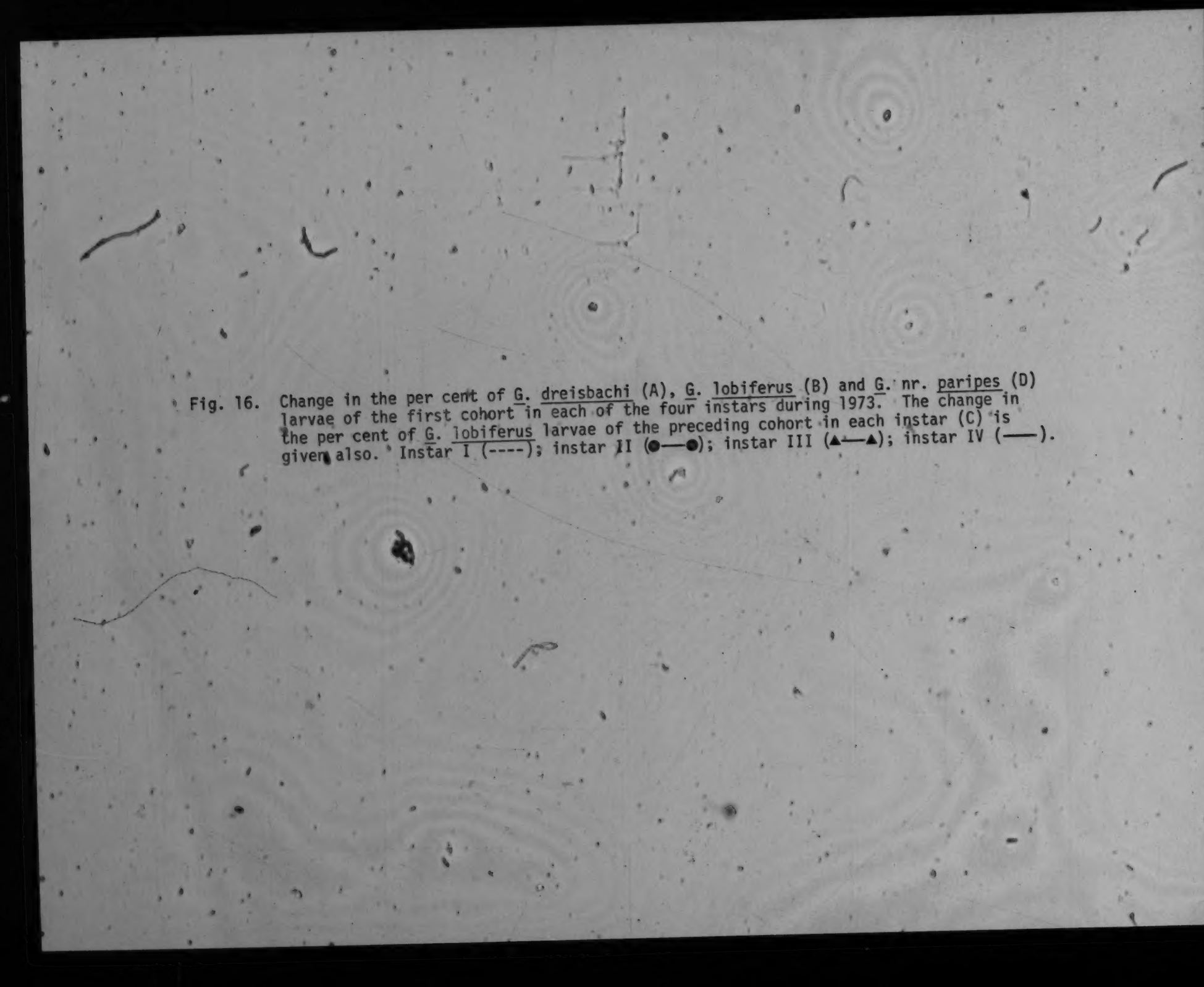


Fig. 16. Change in the per cent of G. dreisbachi (A), G. lobiferus (B) and G. nr. paripes (D) larvae of the first cohort in each of the four instars during 1973. The change in the per cent of G. lobiferus larvae of the preceding cohort in each instar (C) is given also. Instar I (----); instar II (●—●); instar III (▲—▲); instar IV (——).

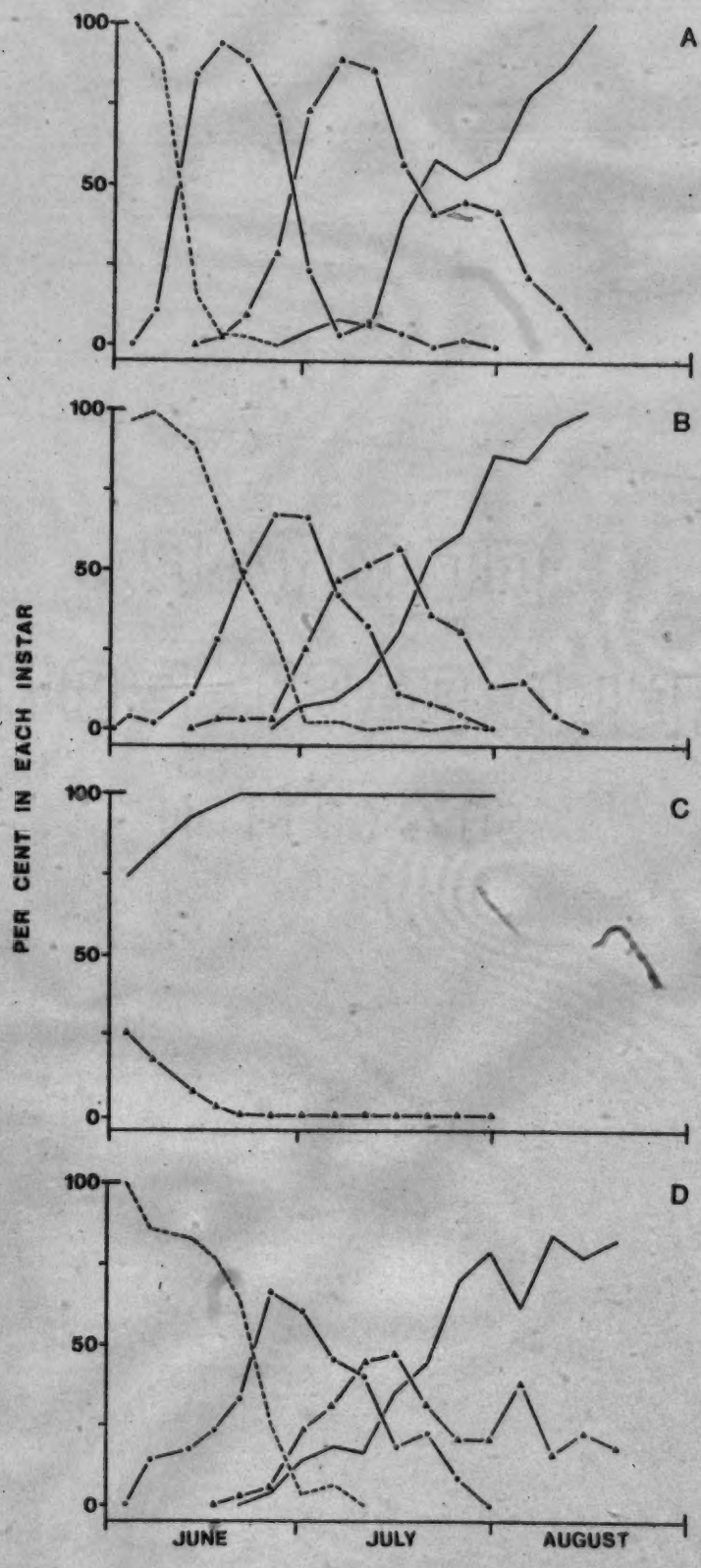

100
50
0
A
B
C
D
PER CENT IN EACH INSTAR
JUNE
JULY
AUGUST

TABLE 17. Life table for G. dreisbachi for its first cohort in 1973. All densities expressed as number per square meter.

Sampling Date	Calendar Age (days)	% Duration of Cohort Completed	Larval Density	Adult Density M	Adult Density F	Total Population Density	Per Cent Population Surviving	Pivotal Age x (days)	No. of Females Surviving to Reproduce	l_x	V_x
May 24	0	0.0	6923.6			6923.6	100.0				
								5.0		1.000	
June 3	10	11.1	37.2								
								12.0			
7	14	15.5	196.2								
								17.0			
13	20	22.1	291.5								
								22.0			
17	24	26.5	704.0			704.0	10.2				
								26.0			
21	28	30.9	254.1			254.1	3.7				
								30.5			
26	33	36.5	363.4			363.4	5.3				
								35.5			
July 1	38	42.0	114.7			114.7	1.7				
								40.5			
6	43	47.5	229.9			229.9	3.3				
								45.5			
11	48	53.0	192.5			192.5	2.8				
								50.5			
16	53	58.6	398.9			398.9	5.8				
								55.5			
21	58	64.1	152.7			152.7	2.2				
								60.5			
26	63	69.6	223.2			223.2	3.2				
								65.5			
31	68	75.1	134.9			134.9	1.9				
								70.5			
Aug. 5	73	80.7	36.2			36.2	0.5				
								75.5			
10	78	86.2	35.6	0.0	1.683	37.3	0.5				
								80.5	3.703	0.001	0.260
15	83	91.7	7.3			7.3	0.1				
								85.5			
20	88	97.2	19.4			19.4	0.3				
								90.5			
25	93	100.0	0.0			0.0	0.0				

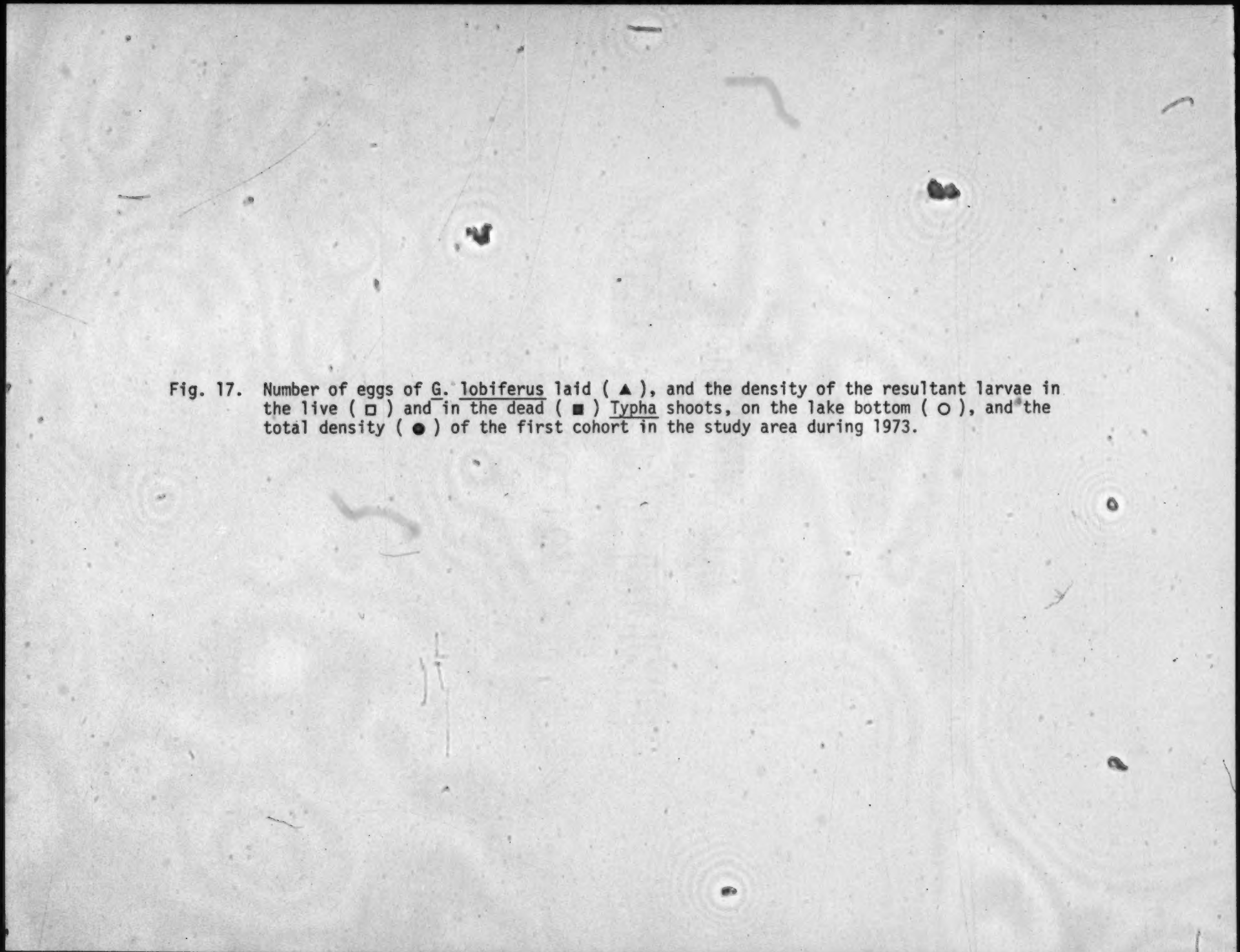
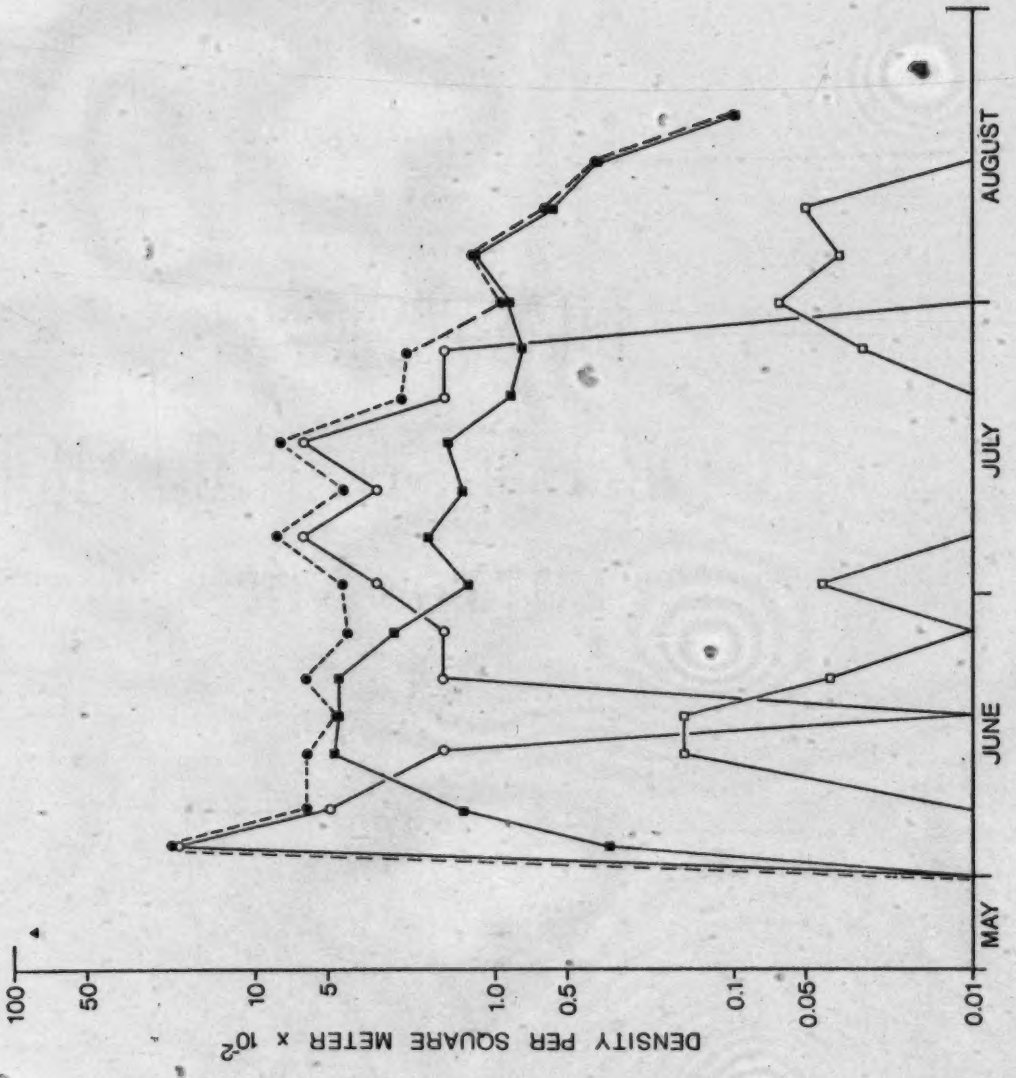


Fig. 17. Number of eggs of G. lobiferus laid (▲), and the density of the resultant larvae in the live (□) and in the dead (■) Typha shoots, on the lake bottom (○), and the total density (●) of the first cohort in the study area during 1973.


DENSITY PER SQUARE METER x 10^2
100
50
10
5
1.0
0.5
0.1
0.05
0.01
MAY
JUNE
JULY
AUGUST

95% confidence limits are given in Appendix III). A plot of the change in the per cent of all larvae in each instar is given in Fig. 16B.

Similar to the preceding two species, the variance of the estimates of total larval density was high (Fig. 13B). Similarly also, calculation of the correlation coefficient between total larval density and time, starting with the peak density (2233.5/m^2 - June 3), revealed a significant decrease in population density ($r = 0.70$, $P \leq 0.01$).

Emergence commenced on June 24 and continued until August 22 (Fig. 14). A total of 53 adults were collected in the traps. Dates for completion of 25, 50 and 75% of emergence were July 13 and 28, and August 12 respectively. Estimates for the number of males, females and both sexes combined which successfully completed the aquatic phase of the life cycle (with the 95% confidence limits in parentheses) were 141.0 (31.9-310.8), 64.2 (34.2-101.3) and 205.2 (85.3-369.7) per square meter respectively.

A life table is given in Table 18, and various population statistics are given in Table 16.

b) Second cohort. A total of five egg masses of the second cohort were found in the egg traps, all during the period August 15-28. As 70 egg masses were deposited by hand in the Typha stand on July 30, and 110 on July 31, all in a regular distribution, the combined numbers being equivalent to a deposition of 0.33 egg masses per 0.1 m^2 (the area sampled by an egg trap), the total number deposited during the period July 30 - August 28 was 11875.0 eggs per square meter. The 95% confidence limits were 6165.4 - 16619.7 eggs per square meter.

TABLE 18. Life table for G. lobiferus for its first cohort in 1973. All densities expressed as number per square meter.

Sampling Date	Calendar Age (days)	% Duration of Cohort Completed	Larval Density	Pupal Density M	Pupal Density F	Adult Density M	Adult Density F	Total Population Density	Per Cent Population Surviving	Pivotal Age x (days)	No. of Females Surviving to Reproduce	l_x	V_x
May 25	0	0.0	8324.2					8324.2	100.0				
										4.5		1.000	
June 3	9	9.7	2233.5					2233.5	26.8				
										11.0			
7	13	14.0	605.5					605.5	7.3				
										16.0			
13	19	20.5	619.7					619.7	7.4				
										21.0			
17	23	24.9	463.4					463.4	5.6				
										25.0			
21	27	29.2	610.1					610.1	7.3				
										29.5			
26	32	34.6	417.1	0.4	2.3	4.7	6.059	430.6	5.2				
										34.5	6.059	0.001	0.670
July 1	37	40.0	447.4	0.0	0.0	3.4	0.337	451.1	5.4				
										39.5	0.000	0.000	0.000
6	42	45.4	818.8	0.0	4.8	0.0	4.788	828.4	10.0				
										44.5	6.194	0.001	0.670
11	47	50.8	449.1	0.0	1.9	11.0	7.400	469.4	5.6				
										49.5	6.054	0.001	0.670
16	52	56.2	788.0	0.0	2.5	2.4	2.356	795.3	9.6				
										54.5	3.030	0.001	0.670
21	57	61.6	242.9	7.7	10.0	11.8	2.356	274.8	3.3				
										59.5	3.030	0.001	0.670
26	62	67.0	237.8	2.0	18.4	20.0	7.733	285.9	3.4				
										64.5	6.327	0.002	1.340
31	67	72.4	93.8	0.0	8.0	32.1	4.570	138.5	1.7				
										69.5	3.164	0.001	0.670
Aug. 5	72	77.8	123.6	1.5	8.0	7.1	1.683	141.9	1.7				
										74.5	3.030	0.001	0.670
10	77	83.2	62.6	3.4	0.0	1.0	0.000	67.0	0.8				
										79.5	0.000	0.000	0.000
15	82	88.6	37.1	6.0	7.7	17.2	17.150	85.2	1.0				
										84.5	15.684	0.004	2.681
20	87	94.0	9.8	2.0	0.0	1.4	1.406	14.6	0.2				
										89.5	0.000	0.000	0.000
25	92	99.5	0.0	2.8	0.0	2.1	0.000	4.9	0.1				
										92.5	0.000	0.000	0.000
26	93	100.0	0.0	0.0	0.0	0.0	0.000	0.0	0.0				

Fifty per cent were deposited by August 15.

First instar larvae of this cohort were found first on August 5. Larvae were found in association with both the live and dead Typha shoots on all except one sampling date (August 10, 1973), but on the lake bottom on only two occasions (September 24, 1973 and February 5, 1974). A plot of the density of the larvae in each sub-habitat, and of the total density on each sampling date is given in Fig. 18 (all density estimates with their 95% confidence limits are given in Appendix III). A plot of the change in the per cent of all larvae in each instar is given in Fig. 19A.

As with the total density estimates for the preceding cohort, those for the present cohort also had a high variance; however, in contrast to the former cohort, calculation of the correlation coefficient as outlined did not reveal any significant ($P \leqslant 0.05$) decrease in population density.

Emergence commenced on June 4 and extended to September 5, 1974 (Fig. 14). Dates for completion of 25, 50 and 75% of emergence were July 4 and 18, and August 8 respectively. Estimates for the number of males, females and both sexes combined which successfully completed the aquatic phase of the life cycle (with the 95% confidence limits in parentheses) were 323.1 (180.6-499.8), 96.5 (9.2-250.0) and 419.6 (179.8-746.5) per square meter respectively.

A partial life table is given in Table 19, and various population statistics are given in Table 16.

4. Glyptotendipes nr. paripes

a) First cohort. Five egg masses were found in the egg traps,

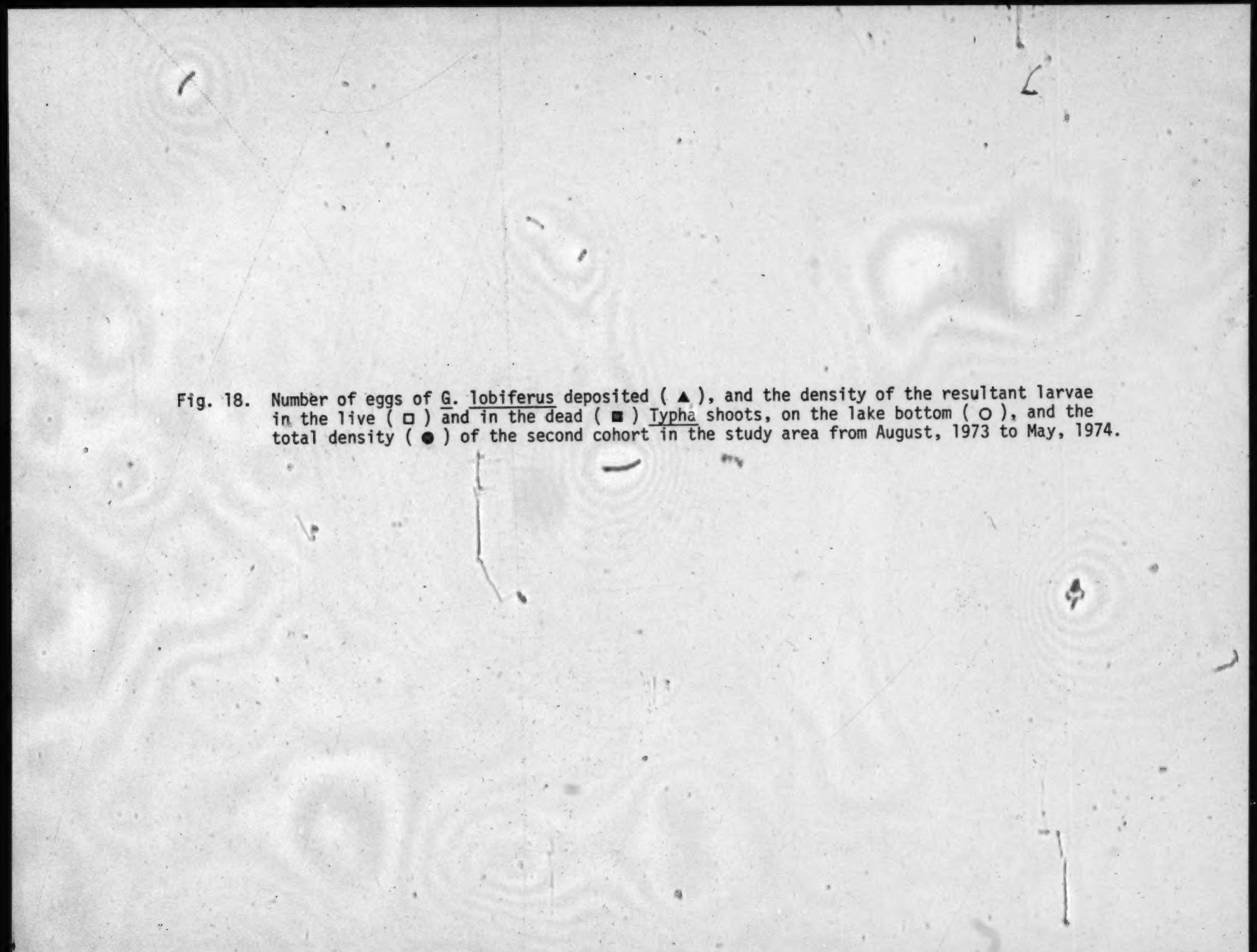


Fig. 18. Number of eggs of G. lobiferus deposited (▲), and the density of the resultant larvae in the live (□) and in the dead (■) Typha shoots, on the lake bottom (○), and the total density (●) of the second cohort in the study area from August, 1973 to May, 1974.

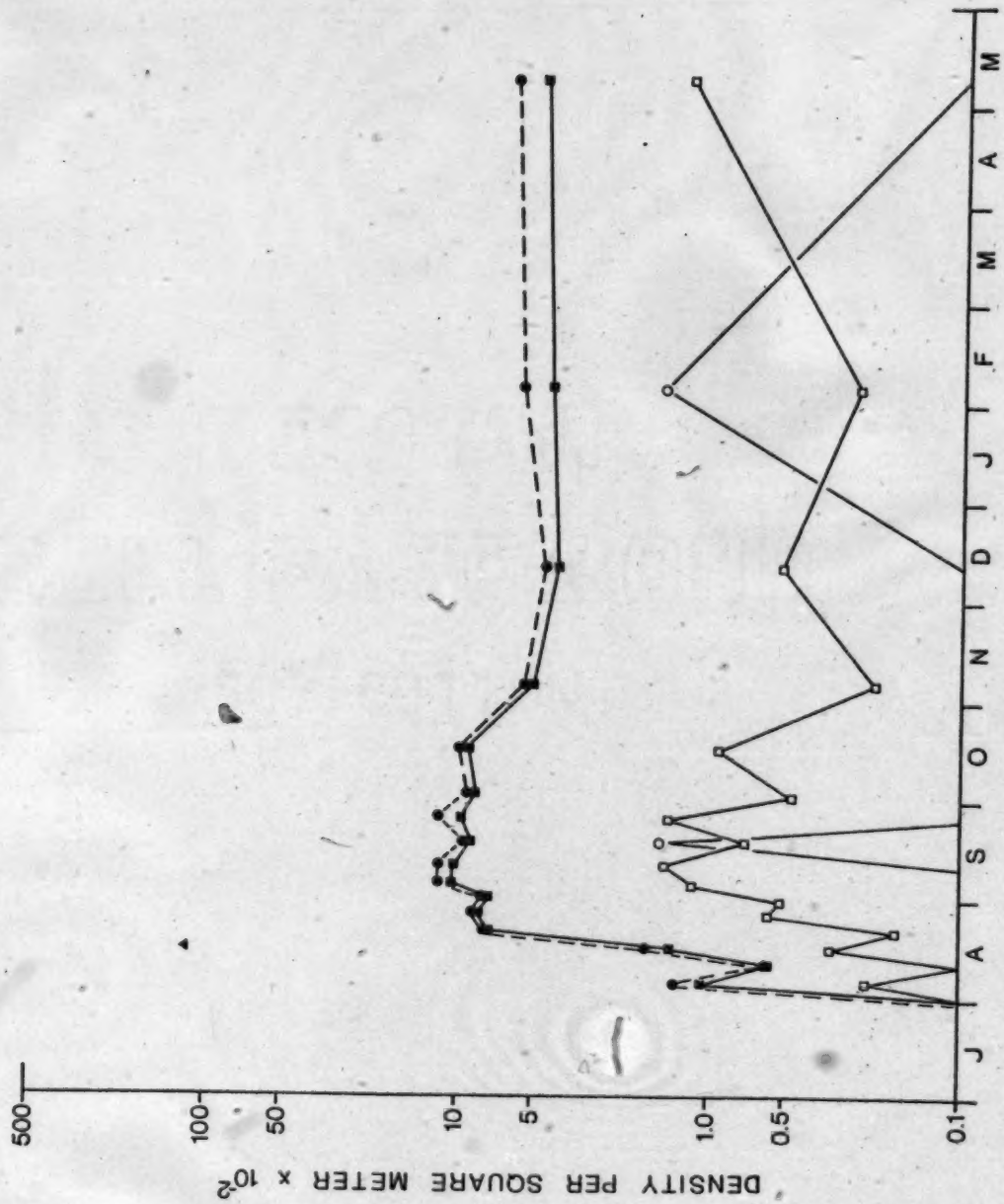

DENSITY PER SQUARE METER x 10^2
500
100
50
10
5
1.0
0.5
0.1
J
A
S
O
N
D
J
F
M
A
M

Fig. 19. Change in the per cent of G. lobiferus (A) and G. nr. paripes (B) larvae of the 1973-74 cohort in each of the four instars. Instar I (----); instar II (●—●); instar III (▲—▲); instar IV (——).

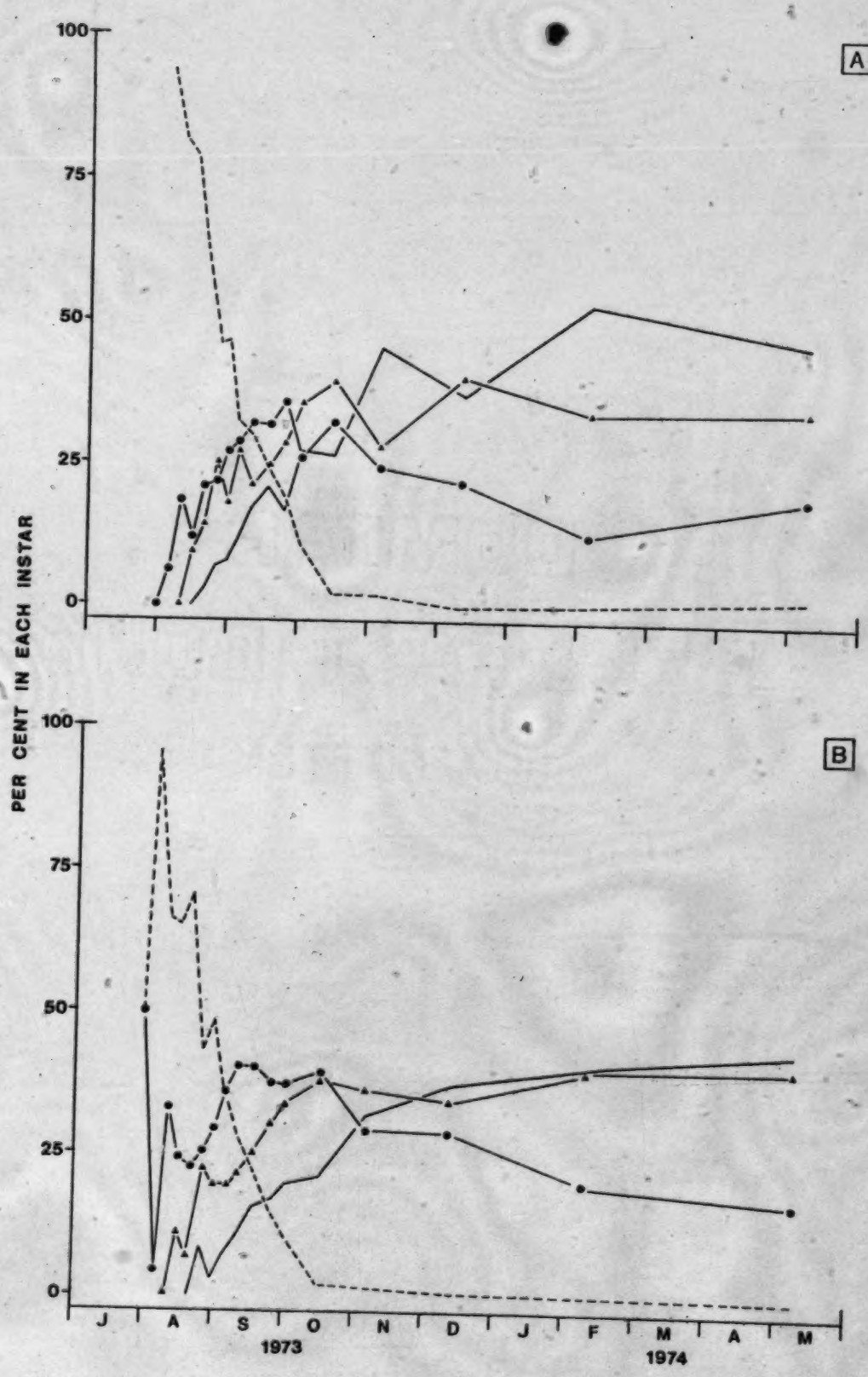

A
B
100
75
50
25
0
PER CENT IN EACH INSTAR
J
A
S
O
N
D
J
F
M
A
M
1973
1974

TABLE 19. Partial life table for G. lobiferus for its 1973-74 cohort. All densities expressed as number per square meter.

Sampling Date	Calendar Age (days)	% Duration of Cohort Completed	Larval Density	Adult Density M	Adult Density F	Total Population Density	Per Cent Population Surviving	Pivotal Age x (days)	No. of Females Surviving to Reproduce	l_x	V_x
Aug. 15	0	0.0	11875.0			11875.0	100.0				
20	5	1.3	745.2			745.2		2.5		1.000	
25	10	2.5	871.9			871.9		7.5			
30	15	3.8	791.3			791.3		12.5			
Sept. 4	20	5.1	1190.8			1190.8		17.5			
10	26	6.6	1186.5			1186.5		23.0			
17	33	8.4	899.2			899.2		29.5			
24	40	10.2	1219.2			1219.2	10.3	36.5			
Oct. 1	47	11.9	859.1			859.1	7.2	43.5			
15	61	15.5	996.4			996.4	8.4	54.0			
Nov. 5	82	20.8	535.7			535.7	4.5	71.5			
Dec. 10	117	29.7	458.7			458.7	3.9	99.5			
Feb. 5	174	44.2	613.5			613.5	5.2	145.5			
May 8	269	68.3	625.3			625.3	5.3	221.5			
June 4	296	75.1		3.9	3.867			280.5			
6	298	75.6		10.2	6.328			297.0	3.164	0.0005	0.312
10	302	77.4		13.7	4.922			300.0	3.164	0.0005	0.312
13	305	77.4		17.4	5.825			303.5	3.164	0.0005	0.312
17	309	78.4		3.3	1.109			307.5	3.328	0.001	0.624
20	312	79.2		16.3	0.000			310.5	0.000	0.000	0.000
25	317	80.5		1.5	0.000			314.5	0.000	0.000	0.000
30	322	81.7		23.2	11.600			319.5	0.000	0.000	0.000
July 4	326	82.7		51.1	11.297			324.0	9.491	0.002	1.248
8	330	83.8		23.7	9.951			328.0	6.654	0.001	0.624
11	333	84.5		5.3	3.515			331.5	6.327	0.001	0.624
14	336	85.3		15.5	3.867			334.5	0.000	0.000	0.000
17	339	86.0		19.2	13.958			337.5	3.164	0.0005	0.312
20	342	86.8		5.5	5.545			340.5	9.982	0.002	1.248
22	344	87.3		16.6	1.109			343.0	0.000	0.000	0.000
25	347	88.1		23.3	4.867			345.5	0.000	0.000	0.000
28	350	88.8		7.4	1.849			348.5	3.328	0.001	0.624
Aug. 1	354	89.8		20.3	12.200			352.0	0.000	0.000	0.000
4	357	90.6		32.4	9.412			355.5	9.982	0.002	1.248
8	361	91.6		14.6	1.055			359.0	3.164	0.0005	0.312
12	365	92.6		21.4	0.000			363.0	0.000	0.000	0.000
16	369	93.6		22.7	0.000			367.0	0.000	0.000	0.000
21	374	94.9		23.0	4.300			371.5	0.000	0.000	0.000
26	379	96.2		27.7	13.291			376.5	3.518	0.001	0.624
31	384	97.5		2.3	1.173			381.5	10.554	0.002	1.248
Sept. 5	389	98.7		3.7	0.000			386.5	0.000	0.000	0.000
9	393	99.8		1.0	0.000			391.0	0.000	0.000	0.000
11	395	100.0		0.0	0.000	0.0	0.0	394.0	0.000	0.000	0.000

all during the period May 22-28. The mean number of eggs laid per square meter was 8410.8, and the 95% confidence limits were 858.2 - 14600.3. Fifty percent of the eggs were laid by May 25.

Similar to G. dreisbachi and the first cohort of G. lobiferus, first instar larvae were not found until June 3. A plot of the density of the larvae in the live and dead Typha shoots and on the lake bottom, and of the total density on each sampling date is given in Fig. 20 (all density estimates with their 95% confidence limits are given in Appendix III). As indicated, larvae occurred in all three sub-habitats but were found least frequently in the live Typha shoots. A plot of the change in the per cent of all larvae in each instar is given in Fig. 16D.

The variance of the estimates of total larval density was high (Fig. 13C); however, a significant decrease did occur in the population density, since calculation of the correlation coefficient between total larval density and time as described previously, gave a value of 0.76 which is significant at $P \leq 0.01$.

Only five male adults were caught in the emergence traps and these emerged between July 20 and August 13. This was equivalent to a survivorship of 18.8 per square meter after the aquatic phase of the life cycle. The 95% confidence limits were 4.8 - 37.8 per square meter.

A life table is given in Table 20, and various population statistics are given in Table 16.

b) Second cohort. A total of five egg masses of the second cohort were found in the egg traps, all during the period August 13-28.

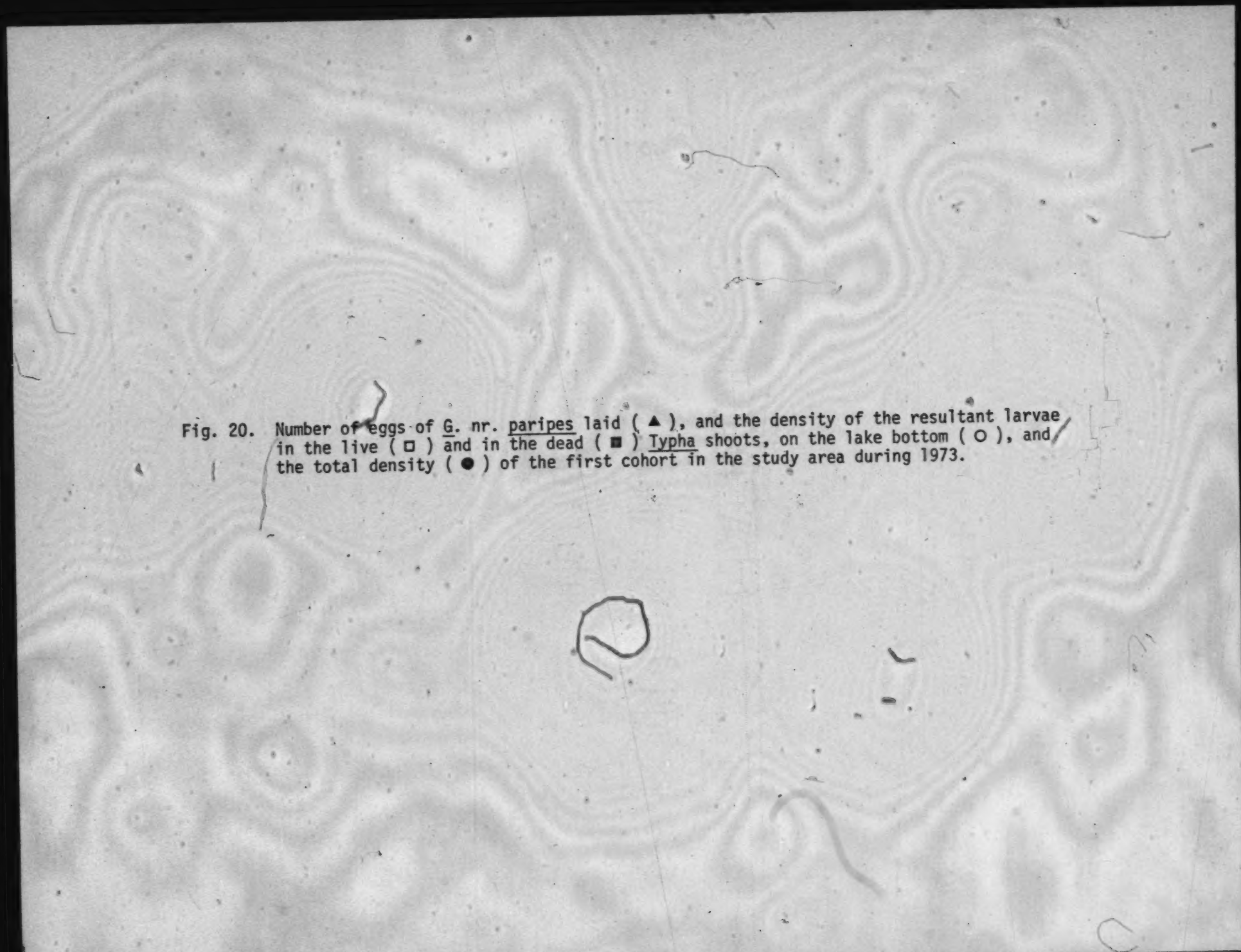


Fig. 20. Number of eggs of G. nr. paripes laid (▲), and the density of the resultant larvae in the live (□) and in the dead (■) Typha shoots, on the lake bottom (○), and the total density (●) of the first cohort in the study area during 1973.

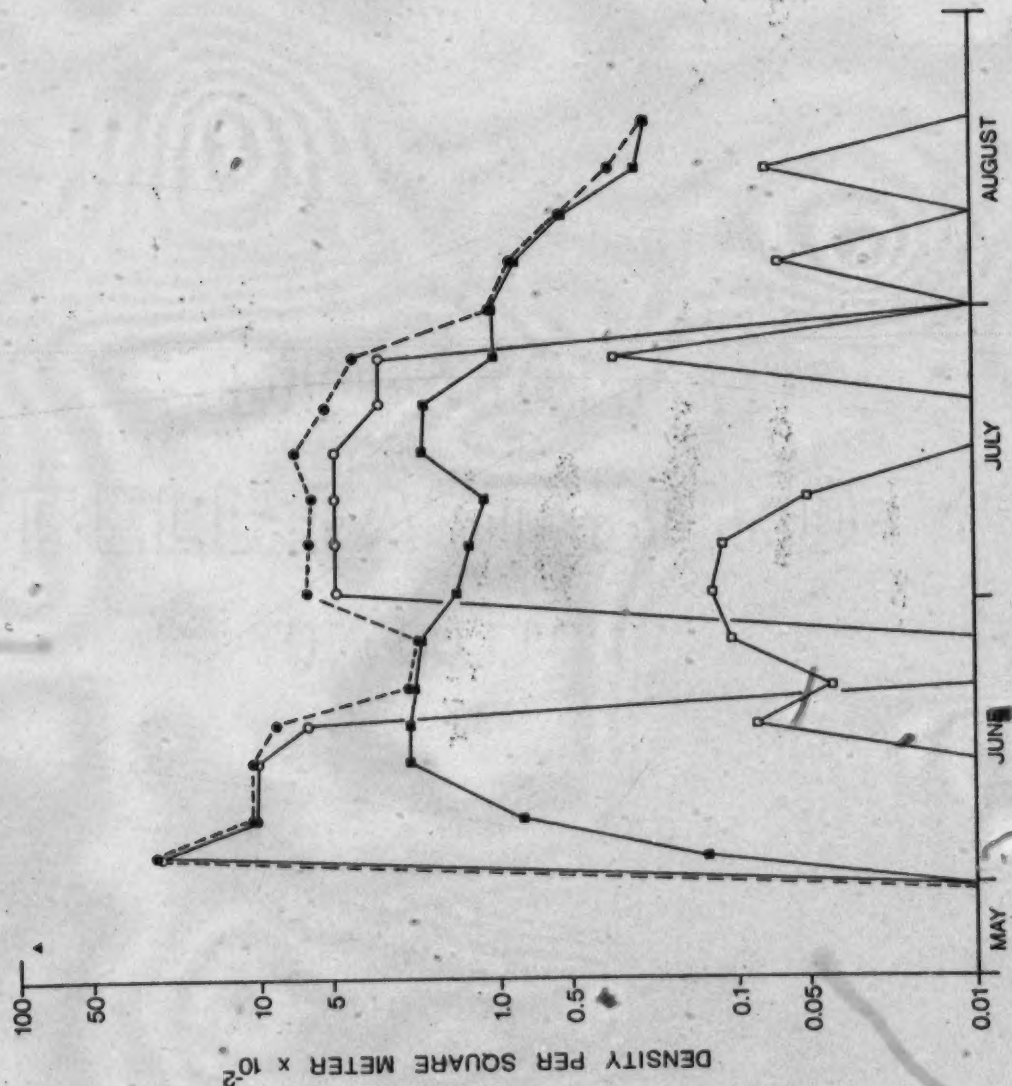

DENSITY PER SQUARE METER x 10^{-2}
100
50
10
5
1.0
0.5
0.1
0.05
0.01
MAY
JUNE
JULY
AUGUST

TABLE 20. Life table for G. nr. paripes for its first cohort in 1973. All densities expressed as number per square meter.

Sampling Date	Calendar Age (days)	% Duration of Cohort Completed	Larval Density	Adult Density M	Adult Density F	Total Population Density	Per Cent Population Surviving	Pivotal Age x (days)	No. of Females Surviving to Reproduce	l_x	V_x
May 25	0	0.0	8410.8			8410.8	100.0				
								4.5		1.000	
June 3	9	10.1	2528.0			2528.0	30.0				
								11.0			
7	13	14.5	1178.8			1178.8	14.0				
								16.0			
13	19	21.2	1179.6			1179.6	14.0				
								21.0			
17	23	25.7	868.9			868.9	10.3				
								25.0			
21	27	30.2	231.8			231.8	2.8				
								29.5			
26	32	35.8	219.1			219.1	2.6				
								34.5			
July 1	37	41.3	632.6			632.6	7.5				
								39.5			
6	42	46.9	612.7			612.7	7.3				
								44.5			
11	47	52.5	594.4			594.4	7.1				
								49.5			
16	52	58.1	684.8			684.8	8.1				
								54.5			
21	57	63.7	522.6	2.4	0.000	525.0	6.2				
								59.5			
26	62	69.3	452.8	3.9	0.000	456.7	5.4				
								64.5			
31	67	74.9	111.6	4.3	0.000	115.9	1.4				
								69.5			
Aug. 5	72	80.4	87.3	3.4	0.000	90.7	1.1				
								74.5			
10	77	86.0	52.2	0.0	0.000	52.2	0.6				
								79.5			
15	82	91.6	32.7	1.7	0.000	34.4	0.4				
								84.5			
20	87	97.2	23.7	0.0	0.000	23.7	0.3				
								89.5			
25	92	100.0	0.0	0.0	0.000	0.0	0.0				

As 60 egg masses were deposited by hand in the Typha stand on July 30, and 120 on July 31, all in a regular distribution, the combined numbers being equivalent to a deposition of 0.33 egg masses per 0.1 m^2 (the area sampled by an egg trap), the total number deposited during the period July 30 - August 28 was 6665.1 per square meter. The 95% confidence limits were 2915.4 - 10153.5 eggs per square meter. Fifty per cent were deposited by July 31.

Larvae of this new cohort were found first on July 31, when two first instar and two second instar larvae were collected in the plant samples. A plot of the density of the new larvae in the live and in the dead Typha shoots, and of their total density on each sampling date is given in Fig. 21 (all density estimates with their 95% confidence limits are given in Appendix III). No larvae were found on the lake bottom. A plot of the change in the per cent of all larvae in each instar is given in Fig. 19B.

Similar to those for the preceding cohorts, the estimates of total larval density had a high variance (Fig. 13F). In contrast to the corresponding cohort of G. lobiferus, calculation of the correlation coefficient between total larval density and time, starting with the peak density (688.1/m^2 - September 10), showed that there was a significant decrease in the population ($r = 0.74$, $P \leq 0.05$).

Emergence extended from May 21 to May 31, 1974 (Fig. 14), and 25, 50 and 75% was completed on May 23. A total of 40 adults were caught. Estimates for the number of males, females and both sexes combined which successfully completed the aquatic phase of the life cycle (with the 95% confidence limits in parentheses) were

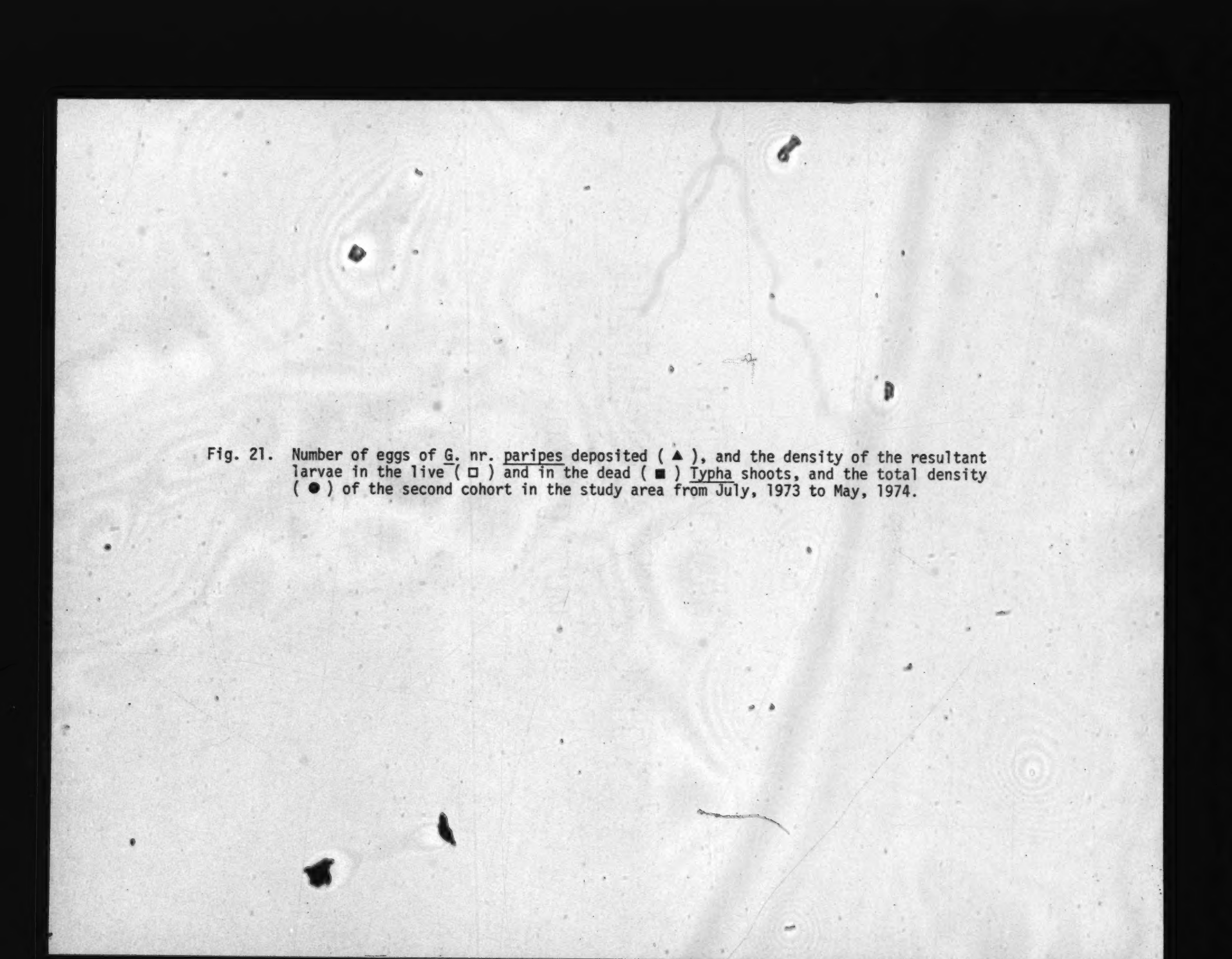
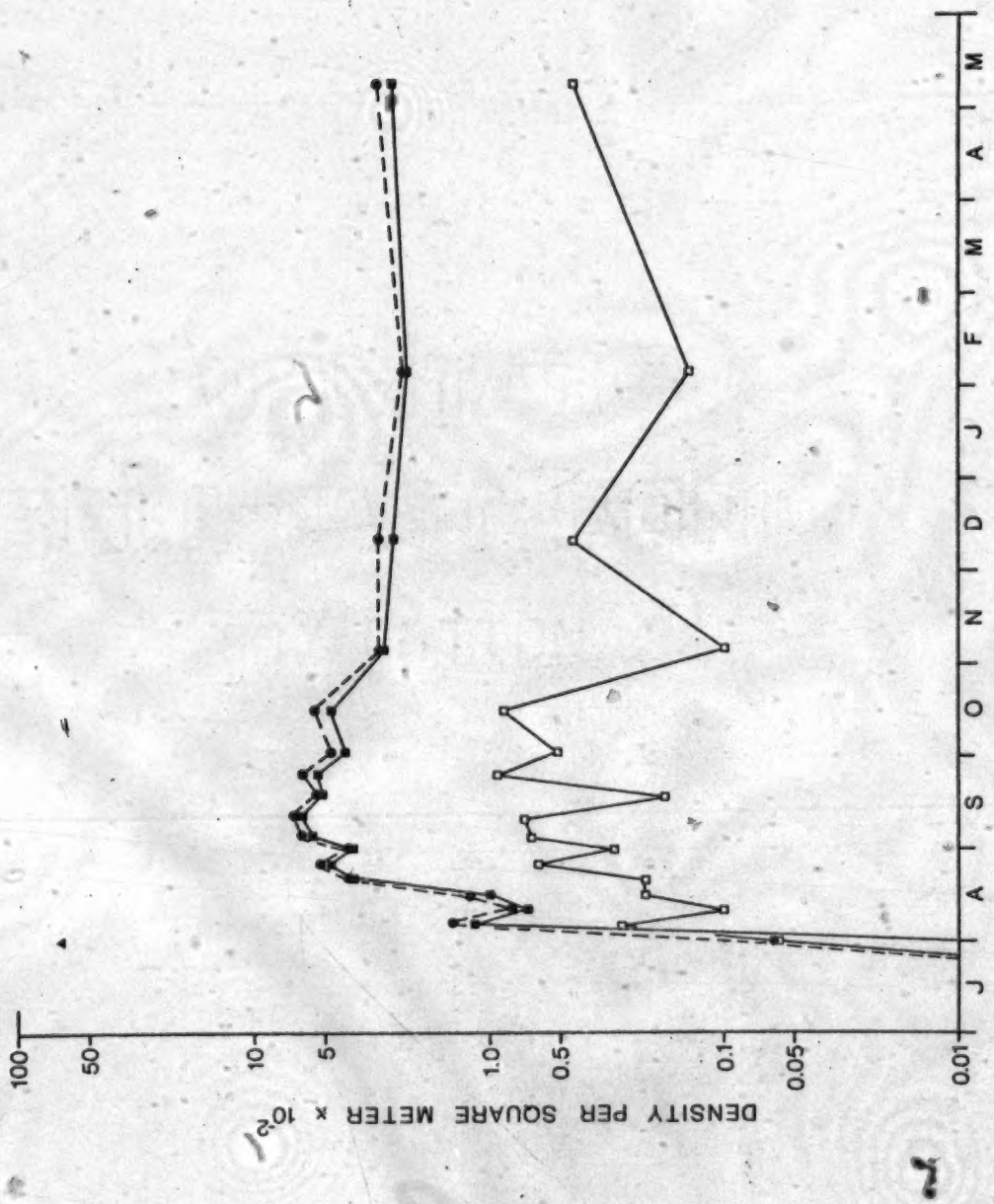


Fig. 21. Number of eggs of G. nr. paripes deposited (▲), and the density of the resultant larvae in the live (□) and in the dead (■) Typha shoots, and the total density (●) of the second cohort in the study area from July, 1973 to May, 1974.


DENSITY PER SQUARE METER x 10^{-2}
100
50
10
5
1.0
0.5
0.1
0.05
0.01
J
A
S
O
N
D
J
F
M
A
M

52.3 (0.3-151.0), 109.7 (6.3-631.0) and 161.9 (28.2-386.9) per square meter respectively.

A partial life table is given in Table 21, and various population statistics are given in Table 16.

F. Mortality Factors.

Results of experiments to determine the hatching efficiency of eggs of G. lobiferus and G. nr. paripes under field conditions are given in Table 22. The temperatures listed are mean values for the duration of each experiment and, except for that with a mean of 24°C, cover a maximum range of 4°C. The experiments with a mean temperature of 24°C were started at 30°C and no trace of any of the egg masses was evident four days later, when the water temperature was 18°C. Results at 16°C are for egg masses placed at the mud-water interface, and with spring collected egg masses; those at the other temperatures are for egg masses placed at the air-water interface and are with summer collected egg masses. Because of the variation in the number and in the time of availability of egg masses of each species, only the experiments at 24°C were performed concurrently.

Larvae of all except the very rare species were found parasitized by mermithid nematodes; however, almost all hosts were either D. nervosus, G. dreisbachi, G. lobiferus or G. nr. paripes. These four species comprised 90-95% of all larvae in the study area.

There was one major peak in the per cent of D. nervosus larvae found parasitized, viz. July 26, 1973, when a value of 32.0% was recorded (Fig. 22). This species exhibited the defense mechanism of parasite encapsulation, but the mean per cent of the hosts in which

TABLE 21. Partial life table for G. nr. paripes for its 1973-74 cohort. All densities expressed as number per square meter.

Sampling Date	Calendar Age (days)	% Duration of Cohort Completed	Larval Density	Adult Density M	Adult Density F	Total Population Density	Per Cent Population Surviving	Pivotal Age x (days)	No. of Females Surviving to Reproduce	l_x	V_x
July 31	0	0.0	6665.1			6665.1	100.0				
								2.5		1.000	
Aug. 5	5	1.6	142.7			142.7					
								7.5			
10	10	3.2	78.6			78.6					
								12.5			
15	15	4.8	121.3			121.3					
								17.5			
20	20	6.4	393.8			393.8					
								22.5			
25	25	8.0	529.4			529.4					
								27.5			
30	30	9.6	403.4			403.4					
								32.5			
Sept. 4	35	11.2	623.0			623.0					
								38.0			
10	41	13.1	688.1			688.1	10.3				
								44.5			
17	48	15.4	527.6			527.6	7.9				
								51.5			
24	55	17.6	628.9			628.9	9.4				
								58.5			
Oct. 1	62	19.9	474.0			474.0	7.1				
								69.0			
15	76	24.4	554.6			554.6	8.3				
								79.5			
Nov. 5	97	31.1	288.9			288.9	4.3				
								114.5			
Dec. 10	132	42.3	296.4			296.4	4.4				
								160.5			
Feb. 5	189	60.6	234.6			234.6	3.5				
								236.5			
May 8	284	91.0	301.4			301.4	4.5				
								288.5			
21	297	95.2		32.5	89.533						
								299.0	73.254	0.022	11.106
25	301	96.5		12.7	24.417						
								302.0	0.000	0.000	0.000
27	303	97.1		10.2	3.867						
								305.0	3.164	0.001	0.505
31	307	98.4		10.2	17.321						
								309.0	13.309	0.004	2.019
June 4	311	99.7		2.2	4.436						
								312.0	0.000	0.000	0.000
6	313	100.0		0.0	0.000	0.0	0.0				

Table 22. Comparison of the hatching efficiency of eggs of G. lobiferus and G. nr. paripes under field conditions.

	Water Temperature (C)			
	16	18	21	24
	Number of Dead Eggs Per Egg Mass			
	Glyptotendipes lobiferus			
	10	1	2	163
	35	3	4	181
	181	35	6	
			7	
			9	
Mean	75.3	13.0	5.6	172.0
Mortality (%)	6.0	1.0	0.4	12.8
	Glyptotendipes nr. paripes			
	2	5	20	158
	4	6	20	179
		11		
		68		
Mean	3.0	22.5	20.0	168.5
Mortality (%)	0.3	2.2	2.0	16.8

Fig. 22. Total number per square meter of larvae of D. nervosus of the 1973-74 cohort (■), the total per cent parasitized by mermithid nematodes (●), and the total per cent parasitized minus the total per cent in which all the mermithids were encapsulated (ϙ).

PER CENT INFECTION
100
75
50
25
0
DENSITY PER SQUARE METER
1000
500
0
J
J
A
S
O
N
D
J
F
M
A
M
1973
1974

all of the parasites were encapsulated was only 0.4%.

G. dreisbachi was parasitized heavily by mermithids. Two infection peaks were recorded, viz. June 13, when 58.5% were found parasitized, and July 21, when a value of 73.4% was recorded. This species also exhibited the defense mechanism of parasite encapsulation, and the mean per cent of the hosts in which all of the parasites were encapsulated was 12.1% (Fig. 23A).

The first cohort larvae of G. lobiferus in 1973 were parasitized by mermithids, and there were two major peaks in the per cent found infected. Similar to G. dreisbachi, the first was recorded on June 13, but the second was recorded on August 15 (Fig. 23B). On the former date 33.1%, and on the latter date 28.6%, of the larvae were found parasitized. These larvae also exhibited the defense mechanism of parasite encapsulation, but not to the same extent as did those of G. dreisbachi; the mean per cent of the hosts in which all of the mermithids were encapsulated was only 0.4%.

G. lobiferus larvae of the 1972-73 overwintering cohort also were parasitized by mermithids. Only three larvae were found parasitized by mermithids which, because of their size, probably entered the hosts in 1973. One was collected on June 7 containing an encapsulated nematode, one on June 13 containing two nematodes, one of which was encapsulated, and one was found on July 21 containing a nematode (Fig. 23C).

Similar to the larvae of the preceding cohorts, those of the second cohort in 1973 also were parasitized by mermithids. There were several peaks in the per cent found parasitized, and the maximum recorded was 28.2% on October 1, 1973 (Fig. 24A). The mean per cent of

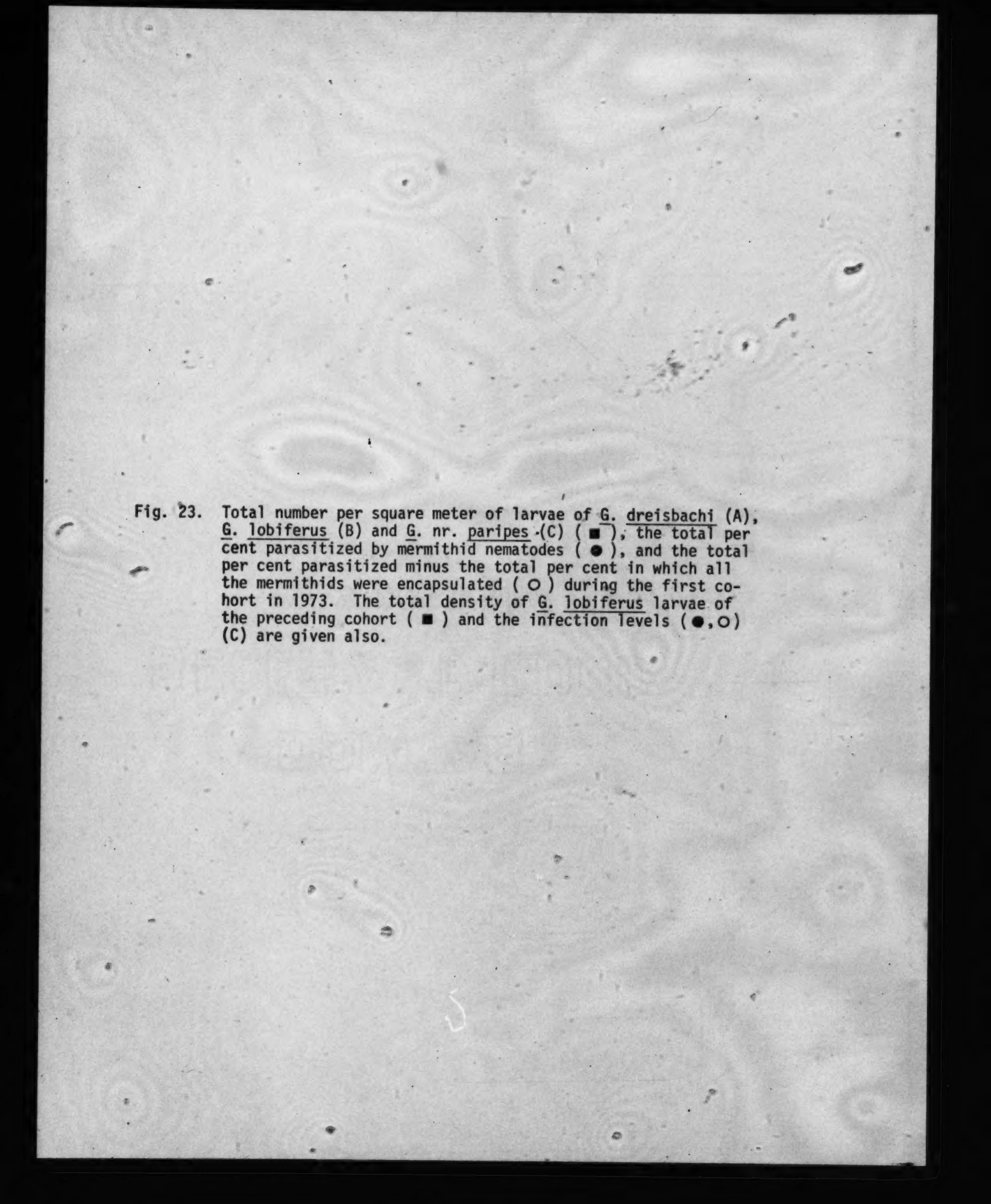
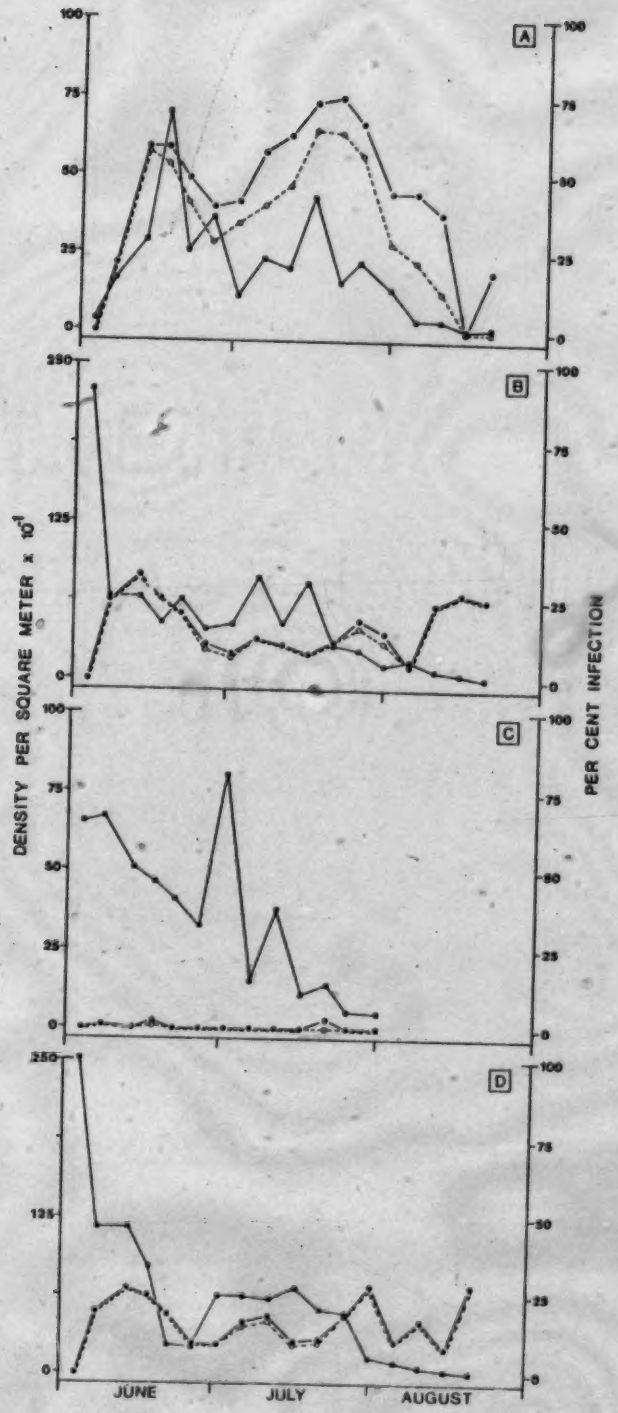


Fig. 23. Total number per square meter of larvae of G. dreisbachi (A), G. lobiferus (B) and G. nr. paripes (C) (■), the total per cent parasitized by mermithid nematodes (●), and the total per cent parasitized minus the total per cent in which all the mermithids were encapsulated (○) during the first cohort in 1973. The total density of G. lobiferus larvae of the preceding cohort (■) and the infection levels (●,○) (C) are given also.


A
B
C
D
DENSITY PER SQUARE METER x 10^{-1}
PER CENT INFECTION
JUNE
JULY
AUGUST

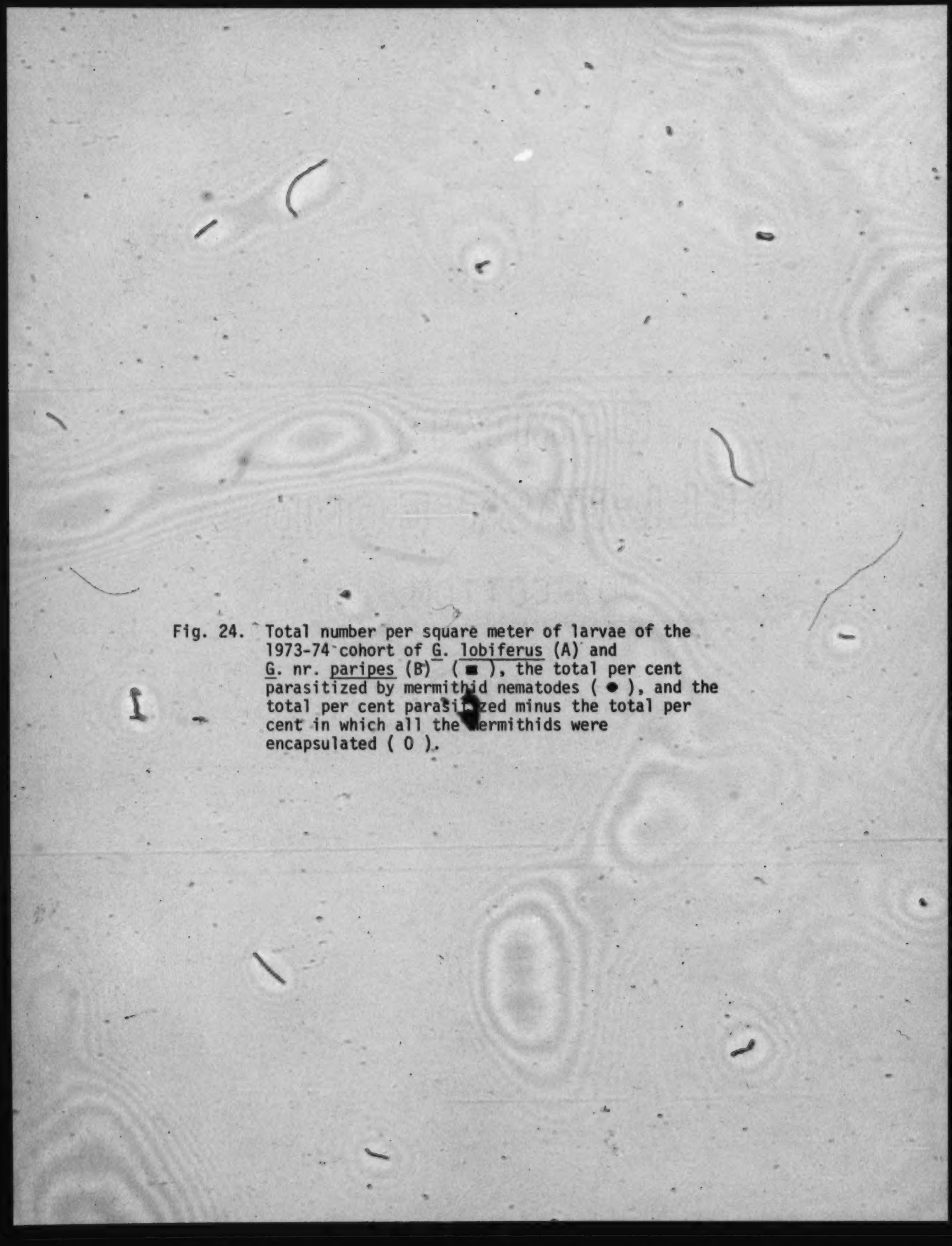
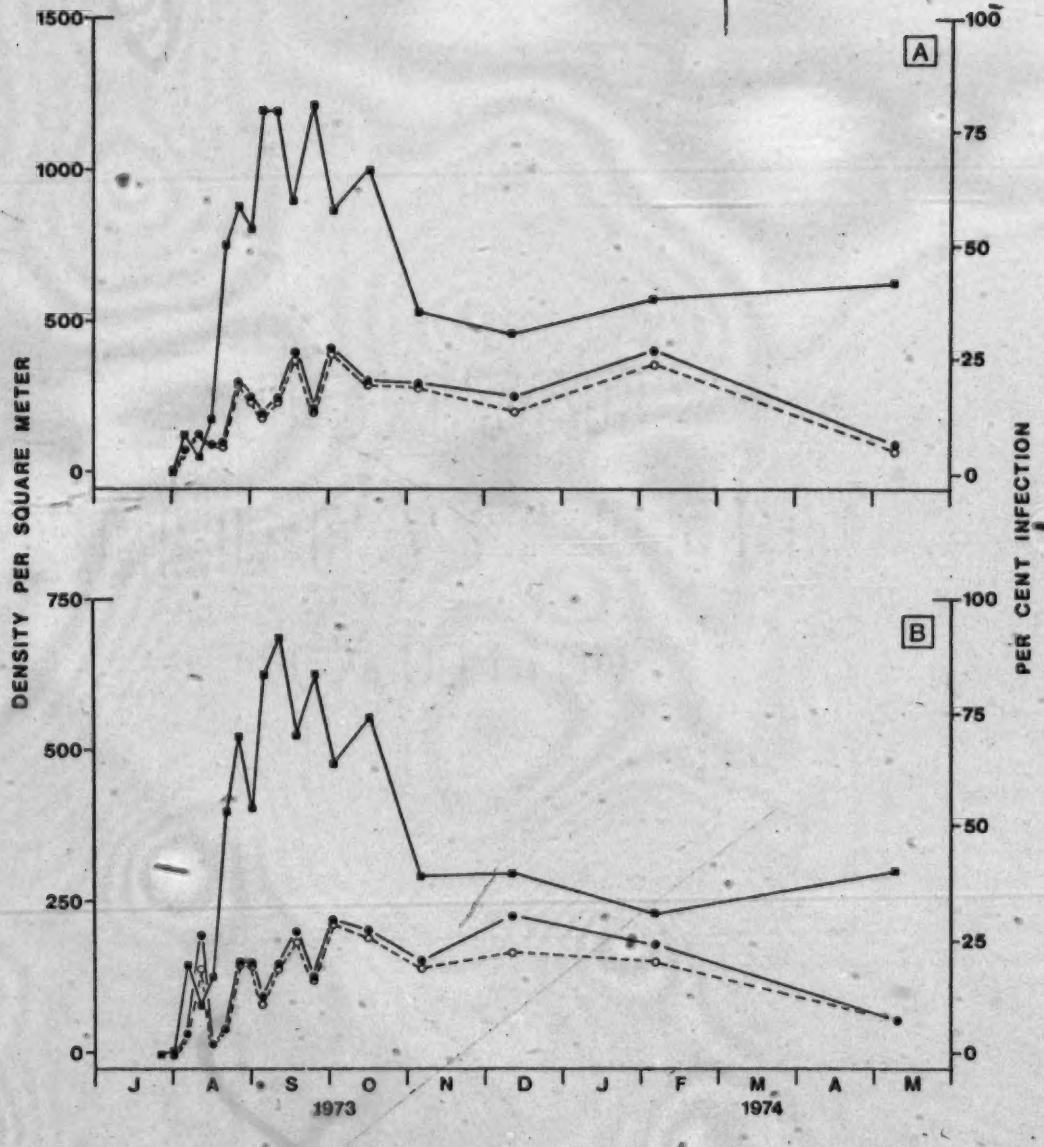


Fig. 24. Total number per square meter of larvae of the 1973-74 cohort of G. lobiferus (A) and G. nr. paripes (B) (■), the total per cent parasitized by mermithid nematodes (●), and the total per cent parasitized minus the total per cent in which all the mermithids were encapsulated (O).


1500
1000
500
0
100
75
50
25
0
A
750
500
250
0
100
75
50
25
0
B
DENSITY PER SQUARE METER
PER CENT INFECTION
J
A
S
O
N
D
J
F
M
A
M
1973
1974

the hosts in which all of the nematodes were encapsulated was 1.2%.

There were four major peaks in the per cent of G. nr. paripes larvae of the first cohort in 1973 which were found parasitized. These occurred on June 13 (27.4%), July 11 (17.7%), July 31 (27.9%) and August 20 (27.3%) (Fig. 21D). Similar to D. nervosus, and to G. lobiferus larvae of the first cohort in 1973, the mean per cent of G. nr. paripes larvae in which all of the parasites were encapsulated was only 0.4%.

Larvae of the second cohort of G. nr. paripes in 1973 also were parasitized by mermithids. Similar to those of G. lobiferus in the corresponding cohort, there were several peaks in the per cent found parasitized. A maximum value of 29.1% was recorded on December 10, 1973. The mean per cent of the hosts in which all of the mermithids were encapsulated was 1.7% (Fig. 24B).

Parasites other than mermithid nematodes were found very rarely in the chironomid larvae. Throughout the study, only six larvae were found parasitized by Microsporida (Protozoa), one by a fungus (Coelomomyces sp. (Blastocladiales)), and one by a nematode tentatively identified as a spiruroid (Spiruroidea).

Examination of all plant samples collected during the period ice was present on the lake to determine the role of low water temperature and/or being frozen in ice as possible mortality factors, revealed the occurrence of very few dead (see Section F in Methods for definition) larvae. Invariably, less than five dead larvae were found on any sampling date. Mortality never was restricted to one species and always was correlated with abundance.

V. DISCUSSION

In the present study four sampling methods were employed in assessing the abundance of the eggs, larvae, pupae and adults of the chironomids. These included submerged inverted funnel traps (= egg traps) for the eggs, a corer and a plant sampler for both the larvae and the pupae, and emergence traps for the adults. The reliability of each method will be discussed.

Few data have been published on the egg laying habits of chironomids. They tend to indicate that the female just flies or bobs low over the water surface and expels the egg mass, and does not exhibit any real selection in the oviposition site (cf. Nielsen, 1962). Although egg masses have been found attached to pieces of floating plant or debris, this may be simply a result of the adhesive nature of the jelly in which the eggs are embedded. In the absence of something to adhere to, egg masses probably sink to the bottom soon after being laid. Such has been reported for those of Glyptotendipes paripes Edwards (Nielsen, 1962).

In view of the above, especially since Nielsen's observations were on a species of Glyptotendipes, the fact that 1) the study area was well protected from wind and wave action, 2) the egg traps were maintained 1-2 cm below the water surface, and 3) an attempt was made to keep the study area free from floating debris, it is believed that the egg traps provided an unbiased estimate of the number of egg masses laid in the Typha stand.

A modified Kajak corer (Kajak, 1965) was used to collect any

larvae and/or pupae on the lake bottom as a corer is considered in most instances to be the best for collecting representative benthos samples (cf. Brinkhurst, 1967). Additionally, as the dispersion pattern of most benthic invertebrate populations appears to be contagious, a small sampling unit is more efficient statistically than a large one (Elliott, 1971). A new sampler was developed for sampling the larvae and pupae in the Typha shoots as none of the existing designs was considered suitable for one or more reasons (McCauley, In Press a). The rapid delimitation of each plant shoot, its collection in its entirety, and in accompaniment with the surrounding water, probably resulted in few of the invertebrates associated with it escaping.

As described previously (Methods - section D), the number of larvae collected in the live and the dead plant shoots was adjusted and expressed always in terms of the Standard Plant Volume (S.P.V.) before calculating the number per square meter. Expressing the density of the larvae always in terms of a constant volume of plant (S.P.V. = 251 cc) must have resulted in overestimating their density in the live plants early in the growing season, and underestimating it late in the growing season. No estimate can be made of this error as no significant change was found in the volume of the live shoots collected throughout the summer. As many of the live shoots had grown sufficiently to protrude through the water surface by late May, 1973, when the chironomids oviposited in the study area, and since the only part of each plant shoot sampled was that between the air-water- and the mud-water-interface, the degree of over- and under-estimation of

the larval density in the live shoots probably was minimal.

All core samples were sifted through a 180 μ mesh sieve, and the water from all plant samples was strained through a 156 μ mesh sieve to maximize retention efficiency (identical sizes in brass and nitex were not obtainable at the start of the study). Although no tests were performed to determine the efficiency of either mesh size for retaining the first instar larvae, results from a previous study (McCauley, 1974) showed that there was no significant difference ($P \leq 0.05$) in the number of such larvae retained in sieved and unsieved samples, using a mesh size of 177 μ and specimens which had been killed by freezing. Despite the smaller (156 μ) mesh size of the sieve which was used in the field to strain the water collected with each plant shoot, first instar larvae may have been lost as they were alive, and the width of their head capsule was about 130 μ. Since the water was strained rapidly and the sieve was vibrated very little, losses may have been minimal. All plant samples were sorted live to maximize extraction efficiency of the chironomids; however, because of the time required for this and other aspects of the study, and the high sampling frequency, the core samples had to be preserved for subsequent examination.

The emergence trap used appears to provide reliable results. The data obtained in experiments to determine its trapping efficiency show that only for Endochironomus n. sp. did the efficiency differ significantly from 100% (Tables 5, 7 and 9). This may have resulted simply from the dispersion pattern of the species on the bottom of the swimming pool. Alternatively, it could have resulted from a shading effect by

the traps, the difference between the species being due to Endochironomus n. sp. emerging when the lights were on and the other two species emerging in darkness. Under field conditions chironomids frequently emerge after sunset, but many species emerge during daylight (Oliver, 1971). If a shading effect by the trap was involved it is doubtful that it would exert a significant effect in the Typha stand because of the greater shading effect by the plants and the high turbidity of the water (Fig. 7). Under field conditions, the number of specimens emerging inside the traps could be affected by water currents. In view of the sheltered nature of the study area and the tendency for many species of chironomids to emerge after sunset when conditions frequently are calmer (no data were gathered on the species in the Typha stand), such an effect may have been minimal.

In the case of the retention efficiency, neither method tested, viz. addition of a constant number of specimens each day, and addition of all specimens at one specific time, is truly representative of that occurring in the field; however, as there was no significant correlation between the number of adults placed in the trap and the per cent retention in either case, it is probable that the same result would be obtained for all emergence patterns. As addition of a constant number of specimens to the emergence trap each day approximates field conditions more closely, the regression line obtained for per cent retention and time (Fig. 9) has been used in estimating the true emergence success of each species in the Typha stand (see below). Ideally, experiments on the trapping and the retention efficiency should have been performed also in the field, in different localities and under a variety of

weather conditions. Because of the time required for other aspects of the study, and the fact that it took approximately four months to complete the laboratory experiments, field experiments were not conducted.

Several life tables are necessary covering a number of cohorts of a population to permit determination of the relative importance of the various mortality factors. Since in the present study two of the species were studied for only one cohort and two for only two cohorts, and especially because of the variance of the density estimates, it seems prudent to combine all of the data to construct a generalized survivorship curve from which to estimate mortality rates and the causal factors.

The generalized survivorship curve is given in Fig. 25 and was obtained by plotting the survivorship (total population density as a per cent of the number of eggs laid initially) against the number of days since the beginning of the cohort (as a per cent of the total duration of the cohort (hereafter referred to as cohort time)). Because of the necessity to make certain assumptions and apply certain correction factors to the data to construct the generalized survivorship curve, all will be discussed before considering its implications.

Whilst oviposition by females is extended over a period of time, in constructing life tables it is considered as being concentrated at one point of time (Dublin and Lotka, 1925). Although in life tables all values are expressed in relation to the pivotal age, i.e. the midpoint between two consecutive sampling dates, it is believed more meaningful to consider a cohort as beginning on the date by which 50% of the eggs have been laid, since usage of the mid-point of the egg laying period

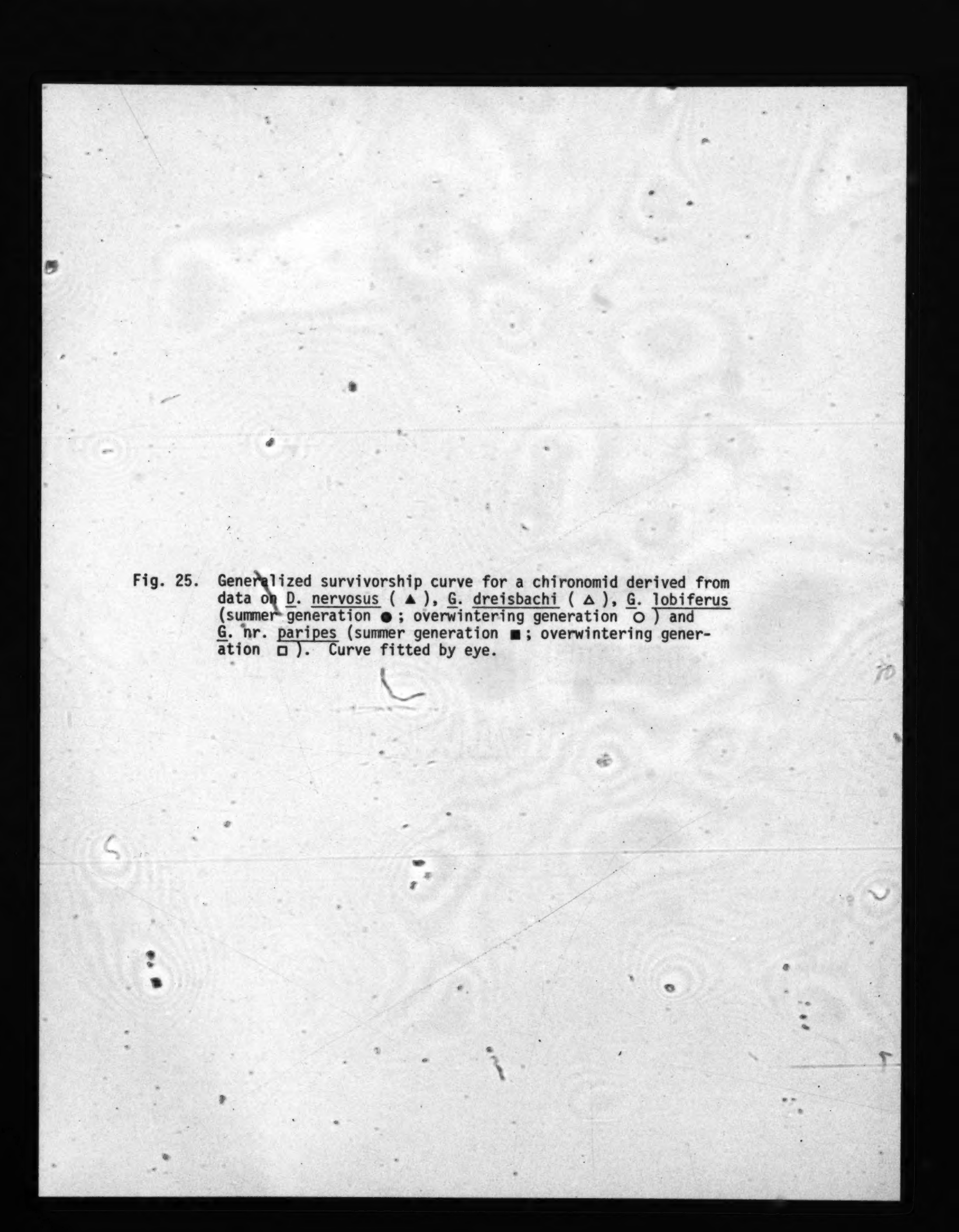
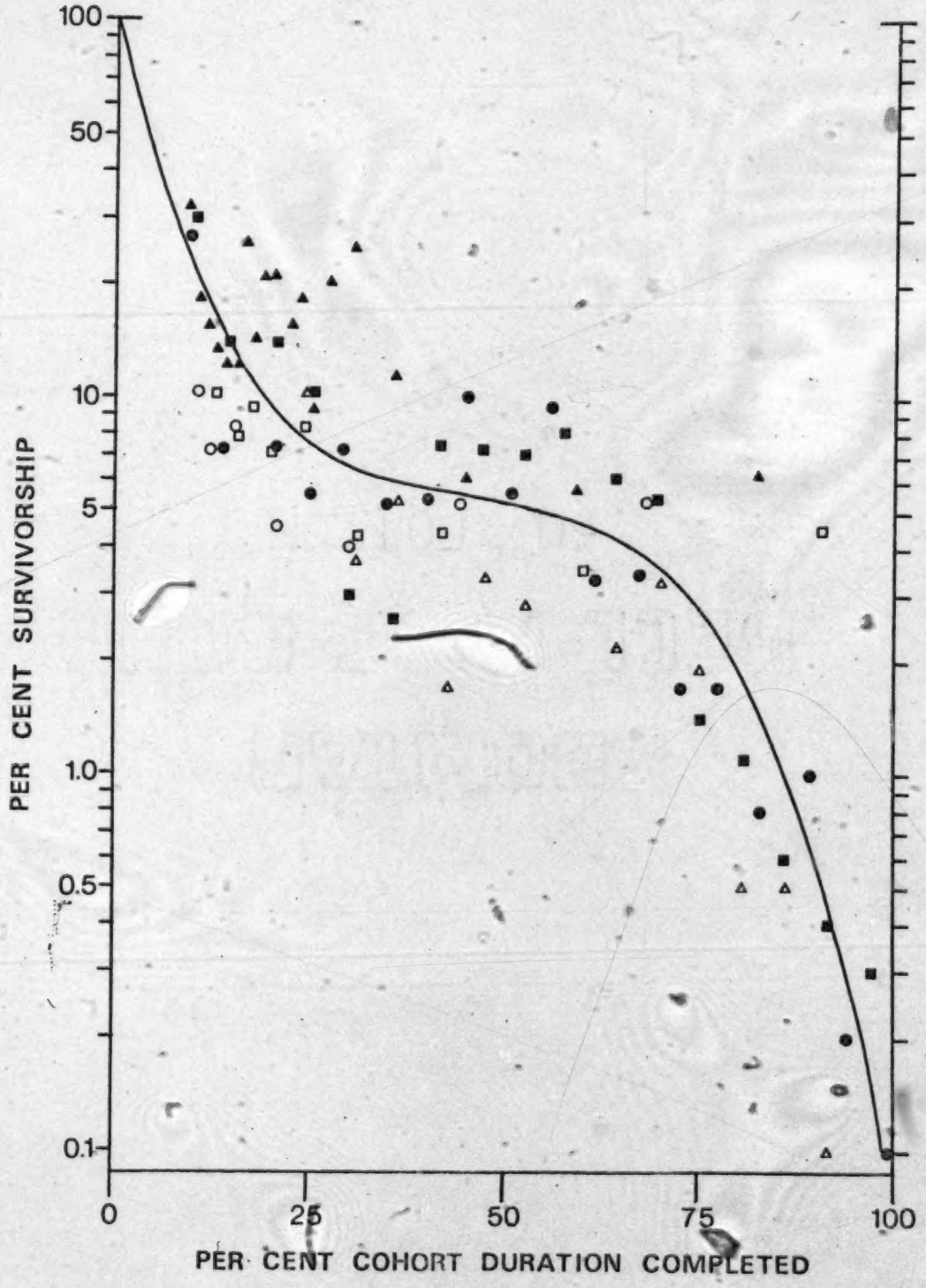


Fig. 25. Generalized survivorship curve for a chironomid derived from data on D. nervosus (▲), G. dreisbachi (△), G. lobiferus (summer generation ● ; overwintering generation ○) and G. nr. paripes (summer generation ■ ; overwintering generation □). Curve fitted by eye.


100
50
10
5
1.0
0.5
0.1
PER CENT SURVIVORSHIP
0
25
50
75
100
PER CENT COHORT DURATION COMPLETED

assumes a constant rate of oviposition. The standard concept of termination of a cohort, i.e. the maximum pivotal age, has been retained.

For all except one of the cohorts (the first cohort of G. lobiferus - Table 18) the total population density represents a summation of the density of just the larvae and the adults. The fact that no pupae of the first cohort of G. dreisbachi or of G. nr. paripes were found most likely was due to few larvae of each surviving to pupate, and to the short duration of this stage. Laboratory rearings at temperatures similar to those in the field indicated that the pupal stage of these and other species lasted only about two days. No pupae of D. nervosus, or of the second cohort of G. lobiferus or G. nr. paripes were found before May 8, 1974, the last date on which plant and core samples were collected.

As discussed in Appendix II, no method was found to differentiate pupae of G. lobiferus from overlapping cohorts; however, as a method was found for the adults, the number of pupae found on each date plant and core samples were collected were divided in the same proportion as was determined for the adults emerging at that time. It is these values which are listed for pupal density. As the plant and core samples were collected every five days during the summer, and as the pupal stage appeared to last only about two days, it is improbable that any specimens would have been in this stage on consecutive sampling dates.

The density values listed for the adults in the life tables have been derived by applying a correction factor to the estimates for the number of specimens which emerged, and subsequently applying a value for their mortality rate. Although a species' emergence rate varies

with time (cf. Fig. 14), it has been assumed that the rate was constant during the period between any two consecutive dates on which the emergence traps in the Typha stand were emptied. Since the emergence traps were emptied usually every two or three days, such an assumption should not be too erroneous.

As discussed previously, the regression line given in Fig. 9 has been used in estimating the true emergence success of each species in the Typha stand. The data used to develop this regression line showed that significantly more females than males were lost from the traps after seven days (Table 12). As no significant difference was found after four days (Table 11), and since the traps usually were emptied more frequently than this, the one regression line has been applied to both sexes.

In the case of the mortality rate of the adults, the data obtained in the 21 experiments to determine the retention efficiency of the emergence trap, based on addition of all specimens at one specific time, showed that the average time required for the death of all adults was five days (range 4-6 days). Since the specimens used in these experiments were a maximum of one day old when initially placed in the traps, the average longevity was 5.5 days. In these experiments also significantly more females than males were lost from the traps (Table 14). This could have resulted from their being attracted to the water surface to lay their eggs, becoming trapped, and subsequently dying there; however, only three egg masses were found during all the experiments to determine the trapping efficiency based on addition of all specimens at one specific time, and only four during all experiments involving the other method. Other behavioral differences could have been involved,

such as intersexual differences in the degree of activity and in response to being confined in a small area. As these experiments were not designed specifically to determine intersexual differences (or even total adult longevity), and since detailed studies by Biever (1967) on the survival of both sexes of three species of chironomids showed no significant ($P \leq 0.05$) intersexual differences, both sexes of G. lobiferus have been assumed to live for the same period of time. Thus the best available estimate for the average longevity of the adult stage of G. lobiferus is 5.5 days. This value is quite similar to those obtained by Biever (1967) for two species of similar size (Goeldichironomus holoprasinus and Chironomus # 51) under similar temperature conditions. In the absence of data on the other three species, a similar longevity has been assumed for them. This may not be too erroneous for two of them as they also belong to the genus Glyptotendipes and are similar in size to lobiferus. For all four species adult mortality has been assumed to be linear with time, since in the experiments to determine the retention efficiency of the emergence trap based on addition of all specimens at one specific time, the best-fit regression line was linear (Fig. 10).

Thus, in summary, on estimating the true emergence success of a species for each period using the regression line in Fig. 9, 81.8% of the adults were assumed to be still alive after one day, 63.6% after two days, etc. As the emergence traps were examined more frequently than at 5.5 day intervals, the values given in the life tables for the density of the adults on each date represent the estimated true number which emerged plus those assumed alive from the previous sampling date(s).

The values listed for the number of females surviving to reproduce

are 81.8% of the number estimated to emerge on each sampling period, since a related species, Glyptotendipes paripes, has been shown by Nielsen (1962) to oviposit one day after emerging.

Despite the fact that the generalized survivorship curve (Fig. 25) is derived from data on four species, on six cohorts which varied in length from approximately 3-13 months and which had estimated starting densities which differed by up to a factor of four, there is only moderate spread in the data. Although the second cohort of G. lobiferus and G. nr. paripes each started with an oviposition period of 28 days, only a small error is involved in estimating the per cent of the cohort time completed by each species using the date by which 50% of the eggs were deposited, since the duration of these cohorts was 394 and 312 days respectively (Tables 19 and 21).

The greatest spread occurs during the period between completion of 15 and 30% of the duration of the cohort. During this period the data for five of the cohorts are similar, but those for D. nervosus suggest a higher survivorship. This may be correct, but also could be due to a second input of eggs to the population, even though none was found in the egg traps. Even if one assumes a greater survivorship by D. nervosus during this period, all cohorts still show a close similarity in their mortality pattern. Mortality appears to be concentrated in early and late life. The generalized survivorship curve suggests that 1) by completion of only 20% of the duration of the cohort only approximately 10% of the initial population is still alive; 2) for approximately the subsequent 60% the mortality rate is low; and 3) for the final 20% it is high. In view of this apparent pattern, mortality in each of the cohorts initially will be considered on the

basis of these three periods.

Field experiments to quantify the hatching efficiency of the eggs were done only with those of G. lobiferus and G. nr. paripes. The results (Table 22) suggest that under the conditions prevailing in the Typha stand in late May, 1973 (data for 16°C), when the first cohort of G. dreisbachi, G. lobiferus and G. nr. paripes started, the the hatching efficiency of the eggs was very high.

No studies were conducted on the role of parasites or predators as agents of egg mortality. Mortality due to parasites probably was minimal, since all of the egg masses collected in the Typha stand, and from various other localities in George Lake (over 100 egg masses in total), for rearing in the laboratory contained very few eggs which did not hatch. Mortality due to predators also may have been low. Potential predators, e.g. leeches and amphipods, were present but not very common during the period in which the eggs were laid. Although gut analyses were not performed on these specimens, results from a previous study in another lake involving analyses of leeches, damsel fly and dragon fly larvae, and caddis and chironomid larvae when egg masses were found on the lake bottom, revealed that none of the specimens contained any eggs in their degestive tract.

The hatching efficiency of the eggs also was high under the conditions prevailing in the Typha stand when the second cohort of G. lobiferus and G. nr. paripes began. As explained previously (Methods - section D), 180 egg masses of each of these species were placed by hand in the Typha stand on July 30 and 31. Experiments with egg masses of both species begun at this time gave mortality values only of

approximately 13 and 17% respectively (Table 22 - data for 24°C). Egg mortality due to predation could have been important at this time, since the numbers and kinds of potential predators was much greater than in late May.

No experiments were conducted on the hatching efficiency of eggs of D. nervosus.

Thus it appears that much of the mortality indicated by the generalized survivorship curve to occur in the first 20% of the cohort time probably took place in the larval stage. Examination of the age structure of the larval population of G. dreisbachi and of the first cohort of G. lobiferus and G. nr. paripes (Fig. 16A, B and D) shows that up to the date by which 20% of the cohort time was completed all larvae of each were just in the first two instars (the approximate date for all three species is June 13). On June 13 most (84%) of the larvae of G. dreisbachi were in the second instar, and most of G. lobiferus and G. nr. paripes (89 and 87% respectively) were in the first instar. Consequently, in these three cohorts the high mortality occurred in the first two instars, and for G. lobiferus and G. nr. paripes occurred primarily in the first instar. This mortality could have been due predominantly to the mermithid nematodes, as the largest number and per cent of infections in each of these species was found in first instar larvae. The number of first instar larvae of each species which died as a result of penetration by the juvenile mermithids through the body wall or through the gut, and consequently which were not found, can only be speculated upon.

In the case of mortality due to predation, as mentioned previously

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potential predators were present but not very common in late May and early June. Additionally, they were of a size which would suggest that consumption of first instar larvae (ca. 0.75 mm long) would be accidental, predation more probably being concentrated on the larger and older larvae.

Other factors may have been involved in the mortality of the first and second instar larvae. The oviposition period at the start of all three cohorts was very short (maximum duration 6 days) and took place concurrently, thus suggesting that the larvae of each species were born concurrently and also during a short period. A few first instar larvae of each species were all found first on the same date (June 3). Examination of the distribution of the larvae of each of the three species in each of the three sub-habitats up to the date by which 20% of the cohort time was completed (June 13 - Figs. 15, 17 and 20) shows that G. dreisbachi was found only in the live and dead plant shoots, G. nr. paripes only in the dead shoots and on the lake bottom, and G. lobiferus only in the dead shoots and on the lake bottom on June 3 and 7, but also in the live shoots on June 13. Although this spatial segregation is based only on four samples in each sub-habitat on three sampling dates, the overall pattern for the duration of the cohort is essentially the same, viz. G. dreisbachi was found most frequently in the live shoots and never on the lake bottom, whereas G. lobiferus and G. nr. paripes were found most frequently in the dead shoots and on the lake bottom.

This spatial segregation could have resulted from competition and, in the process, caused a high mortality of the larvae. If competition was the causal factor, then it appears that it occurred in the

dead plant shoots, since this is essentially the only sub-habitat common to all three species during the first 20% of the duration of their cohorts (a few G. lobiferus were found in one live shoot on June 13).

Competition between these three sympatric cogeneric species could have involved food and/or space. In the case of the former, Hutchinson (1959) found that in various parameters related to the feeding apparatus, sympatric species at the same trophic level ranged in ratio of the larger to the smaller from 1.1 to 1.4. Hutchinson's estimate of a minimum requirement of a 10% difference has been substantiated (e.g. Price, 1972), but there appear to be at least some exceptions (cf. Schoener, 1974). Although no data were collected on the trophic level of any of the three species of Glyptotendipes in the present study, information in the literature on several species in this genus (Burtt, 1940; Leathers, 1922; Thienemann, 1954; Walshe, 1951) indicates that they obtain their food either by browsing, or by periodically filter feeding using a mucous net to trap the food particles, and subsequently eating the net. No selection of a particular type of food has been reported.

In view of the above, the measurements made on the width of the mentum, length of the mandibles, and of the distance from the apex of the mentum to the posterior ventral edge of the head capsule in the mid line (Figs. 49-51 and Tables 2-4 in Appendix I) have been used to calculate trophic indicator ratios between each pair of species. The results are given in Table 23. Assuming a requirement of a minimum difference of about 10% to coexist syntopically, then there was the

Table 23. The three sets of trophic indicator ratios between the three species of Glyptotendipes. Data from Tables 2, 3 and 4 in Appendix I. Length of 'c' represents the distance from the apex of the mentum to the posterior ventral edge of the head capsule in the mid line.

Species	Width of Mentum				Length of Mandible				Length of 'c'			
	Instar				Instar				Instar			
	I	II	III	IV	I	II	III	IV	I	II	III	IV
G. lobiferus / G. nr. paripes	1.02	1.03	1.12	1.07	1.00	1.13	1.21	1.08	1.08	1.22	1.36	1.31
G. nr. paripes / G. dreisbachi	1.11	1.40	1.45	1.46	1.09	1.36	1.56	1.73	1.04	1.18	1.27	1.29
G. lobiferus / G. dreisbachi	1.14	1.43	1.62	1.56	1.09	1.55	1.88	1.88	1.13	1.44	1.73	1.70

potentiality for competition between all three species when in the first instar, especially between G. lobiferus and G. nr. paripes, but only between these two species when in the second instar (the subsequent instars will be discussed later).

As there is a size difference between larvae in each instar, the most suitable method for estimating competition for space is to express the number of larvae on a volume basis. Since no data were collected on the size of the burrow each instar occupies and defends (all three species are miners), only the volume of the actual larvae could be determined.

Although the only measurements which had been made on all larval instars were total length and head capsule length and width, results from a previous study based on 10 species in the same tribe indicated that the ratio of the width of the body to that of the head capsule of newly killed larvae averaged 1.5 : 1 (range of 1:1 to 2:1). Consequently, this ratio was applied to the species in the Typha stand, all larvae being considered as cylinders. The combined total volume was determined only for G. dreisbachi, G. lobiferus, G. nr. paripes and D. nervosus, as they always constituted at least 90% of all larvae found associated with the dead plant shoots, and were four of the five largest species. No differentiation was made between larvae of different cohorts.

For reasons given previously (Methods - section D), the total volume of the chironomid larvae has been expressed in terms of the Standard Plant Volume.

A plot of the data is given in Fig. 26. If competition for space

Fig. 26. Change in total volume of all larvae of G. dreisbachi, G. lobiferus, G. nr. paripes and D. nervosus per Standard Plant Volume (S.P.V.) in the dead plant shoots from June 3 to November 5, 1973. The vertical lines represent the 95% confidence limits.

LARVAL VOLUME (mm³) PER S.P.V. x 10⁻²
0
2
4
6
8
10
J
J
A
S
O
N

128

did occur during the first 20% of the duration of each of the cohorts, then during this period (the first three data points) one would tend to expect the total larval volume per S.P.V. to show a decrease or, since the larvae were growing, for it to remain about the same. In view of the high variance in the data the correlation coefficient between larval volume per S.P.V. and time was calculated. A value of 0.98 was obtained which is significant ($P \leq 0.05$), indicating that an increase occurred in total larval volume per S.P.V., and thus suggesting that competition for space may not have occurred.

Another indicator of the possible existence of competition between the three species in the dead plant shoots due to space and/or food would be a change in the relative abundance of each, and a corresponding increase or decrease in one or both of the other sub-habitats. No conclusions may be drawn concerning density changes because of the high variance in the density estimation for the larvae in each sub-habitat (Appendix III - Tables 13, 14 and 16).

Few conclusions may be drawn concerning the larval instar(s) of D. nervosus or of the second cohort of G. lobiferus or G. nr. paripes which had the highest mortality, as the larvae were in all four instars (Figs. 12 and 19) for much of the period up to completion of 20% of the cohort time (September 4, November 5 and October 1 respectively). This mixed age structure most likely was due to the relatively long egg deposition periods (18 days for D. nervosus and 28 days for both G. lobiferus and G. nr. paripes).

In the case of D. nervosus, the mortality could have occurred in the second and third instar larvae, as most infections by the mermithids

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were found in these two instars; however, the number which died as a result of the penetration process is unknown. Predation also may have been an important mortality factor during the first 20% of this species' cohort time, since the potential predators were very abundant, e.g. 5-10 leeches and 50-200 amphipods were found associated with many of the dead plant shoots.

There may have been competition for food and/or space which could have resulted in mortality. No data were gathered on the size of the trophic apparatus of this species or on its feeding habits. Even if they were similar to those of the other species, the later date of arrival of this species in the study area, and the consequent population age structure differences, should have minimized competition for food and any associated mortality.

Although the data in Fig. 26 indicate a trend to a decrease in the total larval volume per S.P.V. during the first 20% of this species' cohort time, the decrease need not have been due to competition, but instead to emergence, predation and parasite-induced mortality. No conclusions may be drawn concerning density changes because of the high variance in the estimates for the larvae in each sub-habitat (Appendix III - Table 12).

Mortality during the first 20% of the cohort time (second cohort) of G. lobiferus and G. nr. paripes could have been due to competition between them for food, since the potentiality for such competition exists (Table 23). If mortality did result from such competition, then probably it was greatest in first instar larvae, since the trophic indicator ratios between these two species are closest to unity in

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this age class.

In the case of competition for space, the data on total larval volume per S.P.V. in the dead plant shoots (Fig. 26) indicate a trend to a build-up during the first 20% of each of these species' cohort time. Since, as mentioned previously, one would tend to expect little change or a trend to a decrease, competition for space may not have occurred. As with the preceding cohorts, no conclusions may be drawn concerning density changes in the sub-habitats because of the variance (Appendix III - Tables 15 and 17).

Mortality due to predation could have been important for both species during early life because of the abundance of potential predators.

The water temperature was very high (ca. 30°C - Fig. 8) when both these cohorts were started (Methods - section D). Consequently, there could have been a significant mortality due to it and the concommitant parameters.

The data available on larval survivorship in all six cohorts up to the point that 20% of the cohort-time was completed suggest that much of the mortality may have been concentrated in the first or the first and second instar. This is suggested by the results obtained for G. dreisbachi and for the first cohort of G. lobiferus and G. nr. paripes. Additionally, although trophic indicator ratios could be calculated only between three of the four species, they show that there is the potentiality for competition between them for food and that it is highest between, or even restricted to, specimens in the first instar.

The generalized survivorship curve (Fig. 25) indicates that mortality during approximately the middle 60% of the cohort time was low. The major mortality factors acting on the summer cohorts during this period (G. dreisbachi and the first cohort of G. lobiferus and G. nr. paripes - from June 13 to August 5) may have been parasitism and predation, since potential predators were abundant and all three species were parasitized heavily by the mermithids (Fig. 23) (which are known invariably to cause the host's death when they leave). Competition for food, and any resultant mortality, appears to have been low as suggested by the trophic indicator ratios (Table 23). In the case of competition for space, the data on total larval volume per S.P.V. in the dead shoots indicate a trend to a decrease; however, the variance in the density estimates for larvae in each sub-habitat (Appendix III - Tables 13, 14 and 16) does not permit any conclusions concerning sub-habitat shifts by the species.

In the case of mortality during the corresponding period in the cohorts which overwintered (D. nervosus - September 4 to May 8; second cohort of G. lobiferus - November 5 to June 25; second cohort of G. nr. paripes - October 1 to April 7) no one factor seems to have predominated. Exposure to low water temperatures and being frozen in ice does not appear to have caused significant mortality, since examination of plant and core samples throughout the period ice was on the lake revealed very few dead larvae. Some of these could have died as a result of the shock waves produced when cutting through the ice to sample.

Mortality in approximately the final 20% of the duration of all

cohorts probably was due in part to the involvement of two major metamorphoses (larva to pupa to adult), and in part to parasitism, either as a result of the mermithids leaving their hosts, or because the hosts had insufficient energy reserves for one or both metamorphoses. The only data on efficiency of metamorphosis from the fourth instar larva through the pupa to the adult under field conditions appears to be that by Hunter (1965). He studied Chironomus (= Dicrotendipes) californicus Johannsen and found that of 100 fourth instar larvae divided equally between four submerged cages, only 75% emerged. No indication was given of the variance. Concurrent experiments with specimens parasitized by Gurleya sp. (Microsporida) showed no emergence.

Predation also may have been involved during the final 20% of the cohort time of the summer cohorts, since potential predators were abundant.

The per cent of the specimens of each species which completed the aquatic phase of the life cycle varied from 0.05% for G. dreisbachi to 8.21% for D. nervosus. If the former species is excluded because of the extremely high level of parasitism by the mermithids, the range is one magnitude less (Table 16). The range may be even less, as the value for D. nervosus may be an overestimation. The data for this species (Fig. 13D; Table 15) suggest the possibility of a second input of eggs to the population after completion of about 25% of the cohort time; however, there was considerable fluctuation in the total density and none of the increases was statistically significant.

Although data in the literature would suggest that the generalized

survivorship curve obtained for the four species of chironomids (Type IV - classification according to Slobodkin, 1963) is characteristic of many if not most freshwater invertebrates, the only published data which includes density estimates for the eggs in addition to that for the young, appears to be that for two species of leeches, viz. Glossiphonia complanata (L.) by Mann (1957) and Erpobdella octoculata by Elliott (1973). Both species had Type IV survivorship curves.

Based on a study of survivorship curves of several natural insect populations, Ito (1959, 1961) concluded that the mortality of a species over its entire life span, and the relative proportion which occurs in the early developmental stages, decreases with increasing social evolution (= parental care). Since chironomid females do not appear to exhibit any selection in their oviposition site, but just expel their egg mass into the water, it follows that the survivorship curve should be Type IV.

The population statistics for the chironomids (Table 16) fit in the appropriate location in graphs of the generalized fundamental principles in population dynamics. These include 1) increasing total fecundity accompanying decreasing total survivorship; 2) a hyperbolic inverse relationship between the intrinsic rate of natural increase (r_m) and mean generation time (T); and 3) the positive correlation between body size and mean generation time on a log-log plot (cf. Pianka, 1974).

Few conclusions may be drawn from comparisons of the chironomid population statistics (Table 16) and other data, as all other data are

on laboratory populations. In these other studies predation and parasitism were non-existent, and temperature and food supply were maintained constant. Temperature and food supply, both individually and in interaction, have been shown to influence the intrinsic rate of natural increase of several aquatic invertebrate species (e.g. Stiven, 1962; Hall, 1964; Schiff, 1964; Cooper, 1965; Sturrock, 1966; Schiff and Garnett, 1967; Sturrock and Sturrock, 1972). In the present study a difference of a magnitude of five was found between the intrinsic rate of natural increase for the summer and overwintering cohorts of G. lobiferus. Most of this difference probably was due to temperature, as ice was present on the lake for approximately 60% of the duration of the overwintering cohort.

In considering the various mortality factors which may have influenced the survivorship of each of the six cohorts, it is evident that both density-dependent and density-independent factors were involved; however, the relative importance of each cannot be stated. Density-independent mortality factors are characteristic of unstable and/or unpredictable environments, whereas under more stable and/or predictable environmental regimes much mortality is more directed and favours individuals that are better able to cope with high densities and strong competition. The best strategy in the former case is to produce many offspring, but in the latter it is to produce offspring with more substantial competitive abilities. The latter usually requires larger offspring and, since they are energetically more expensive, fewer can be produced (Pianka, 1974). Additional strategical advantages of the former include a high reproductive rate,

and the ability to disperse in search of new habitats as the existing ones begin to grow unfavourable. MacArthur and Wilson (1967) have designated these two opposing selective forces "r-selection" and "K-selection". There can be no doubt that the four species of chironomids studied can be characterized as r-strategists. The number of eggs per egg mass in the three species of Glyptotendipes is very high as compared to chironomids in general, and that for G. lobiferus is among the highest ever recorded. This high fecundity coupled with the ability to fly probably represents the major reasons for the distribution of this genus being world wide.

The occurrence of the three species of Glyptotendipes in the same habitat is of particular interest. Although the degree to which they compete is unknown, there is evidence of ability to co-exist through niche specialization. There appears to be different spatial utilization of the sub-habitats. Additionally, there is morphological character displacement as shown by the trophic indicator ratios - there may be both food size and kind differences, since the mentum of G. dreisbachi is markedly different from that of G. lobiferus and G. nr. paripes in the final three instars.

The role of competition in influencing the duration of the cohorts is uncertain. Various data tend to indicate that G. lobiferus is competitively superior to G. nr. paripes. This is suggested by some of the population statistics (Table 16), and by the change in the proportion of specimens of each species in the same instar in a particular sub-habitat. In the case of the latter, an examination of the dead plant shoots showed that during the highly synchronized first

cohort, the number of G. lobiferus in the first, second and third instar divided by the number of G. nr. paripes in the corresponding instars followed a general positively skewed pattern; initially G. lobiferus was more abundant but, with time, G. nr. paripes became more abundant (Fig. 27). The repetition and synchrony of this pattern suggests that G. lobiferus out-competed G. nr. paripes for the available resources in each instar and hence metamorphosed into the subsequent instar sooner. The same pattern may have occurred in the fourth instar also, but was not demonstrated because of some of the specimens having emerged. A similar type of positively skewed pattern appears to occur also in the second cohorts of these species (Fig. 28), but is not as well defined. This may be due to the long egg deposition periods (28 days for both species), the consequent probable lack of synchrony between corresponding instars of the two species, and hence a minimizing of competition between them.

Despite the above indications, the duration of the overwintering cohort of G. lobiferus was 394 days and that of G. nr. paripes was 312 days. In view of the results of detailed experiments on Chironomus nuditarsis Strenzke and C. plumosus (Linnaeus) by Fischer (1974), it seems likely that dormancy[5] is involved. Fischer studied one population of the former and two of the latter species and found that a dormancy phase could occur in all three at the end of the fourth instar. Both long and short days caused some of the larvae in each of the three populations to cease development. The check in development induced by

[5]Dormancy is every stop or retardation of development which appears (facultative or obligatory) in the ontogeny of an insect (Thiele, 1971).

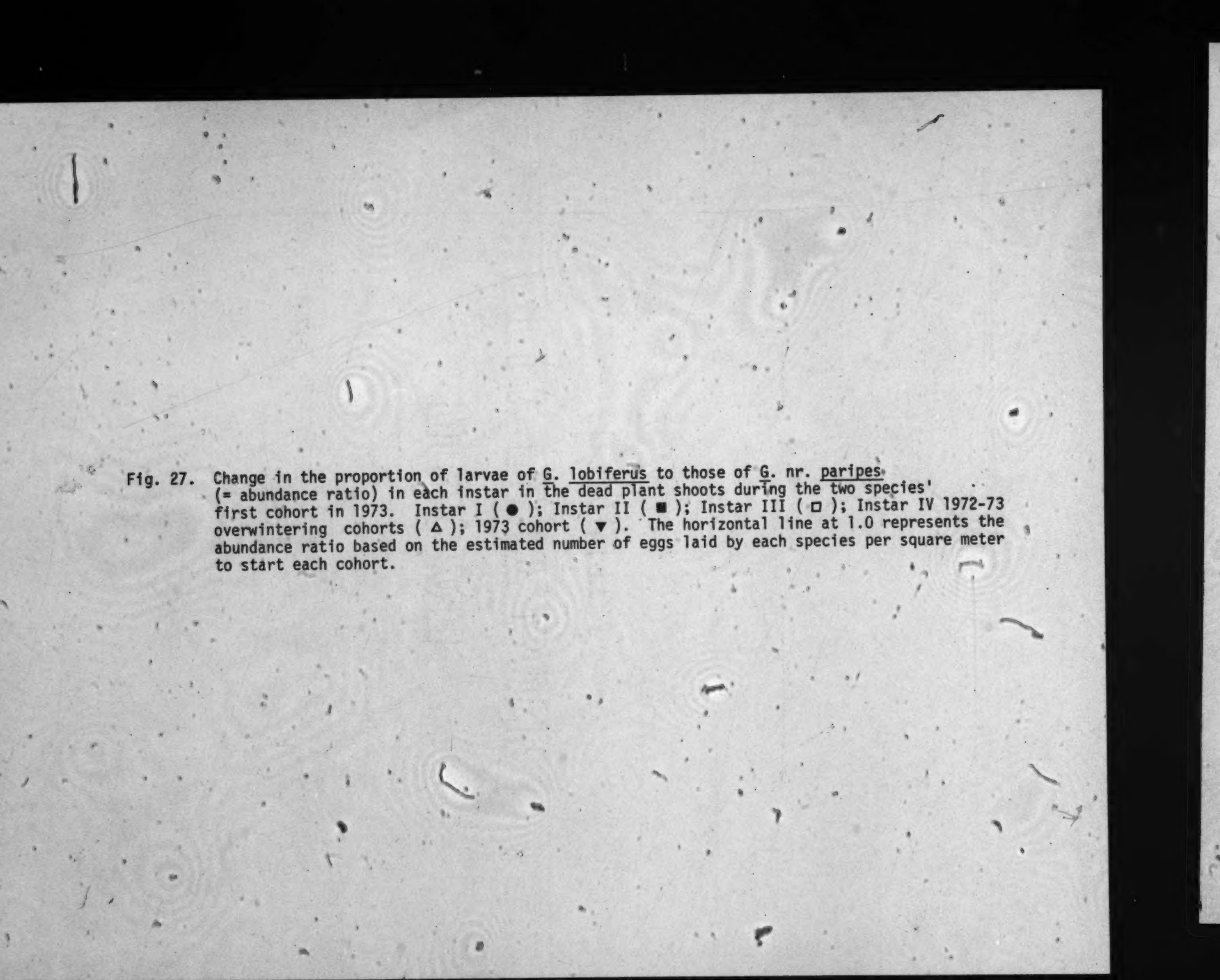


Fig. 27. Change in the proportion of larvae of G. lobiferus to those of G. nr. paripes (= abundance ratio) in each instar in the dead plant shoots during the two species' first cohort in 1973. Instar I (●); Instar II (■); Instar III (□); Instar IV 1972-73 overwintering cohorts (△); 1973 cohort (▼). The horizontal line at 1.0 represents the abundance ratio based on the estimated number of eggs laid by each species per square meter to start each cohort.

ABUNDANCE RATIO
10.0
7.5
5.0
2.5
0
39.0
JUNE
JULY
AUGUST

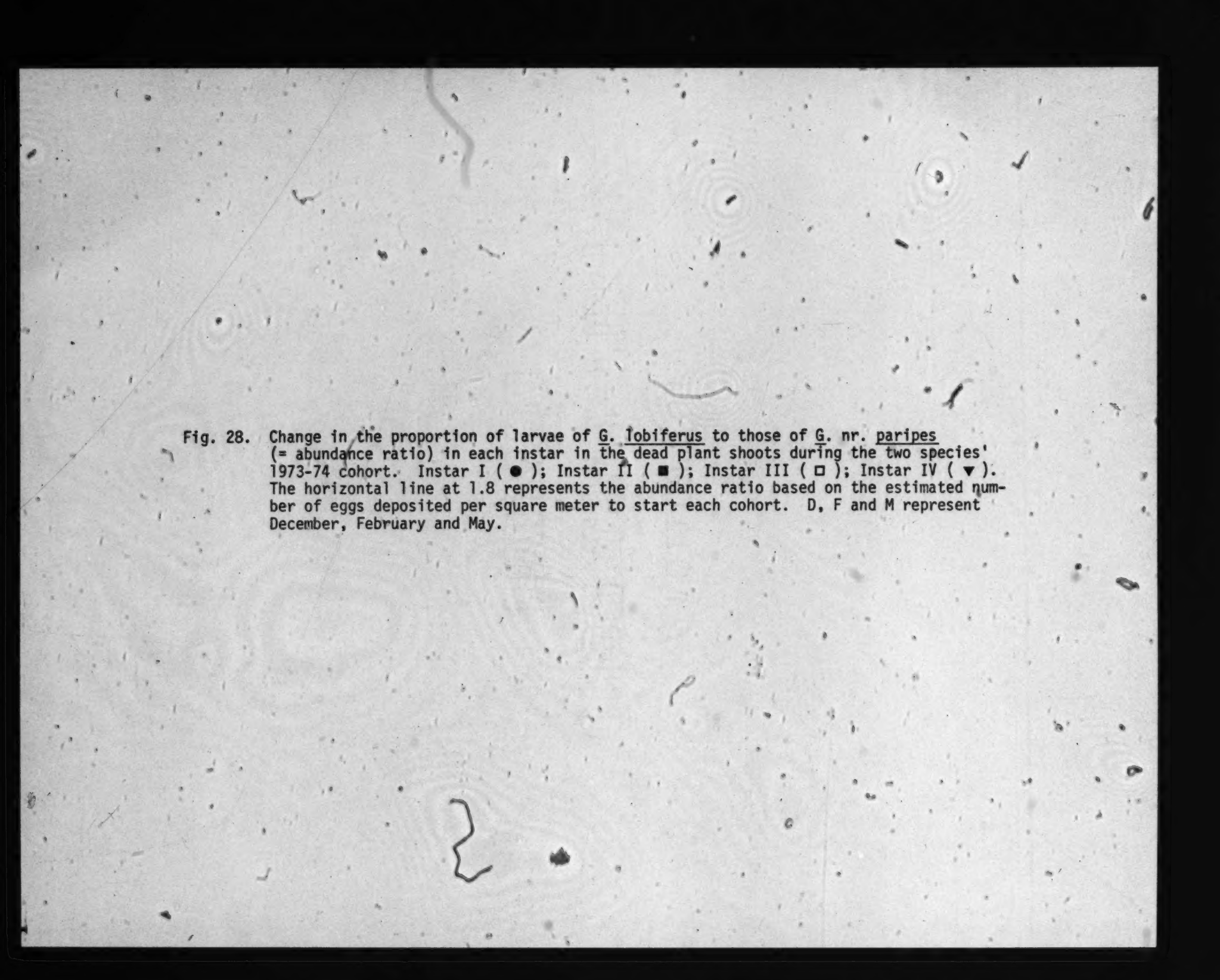
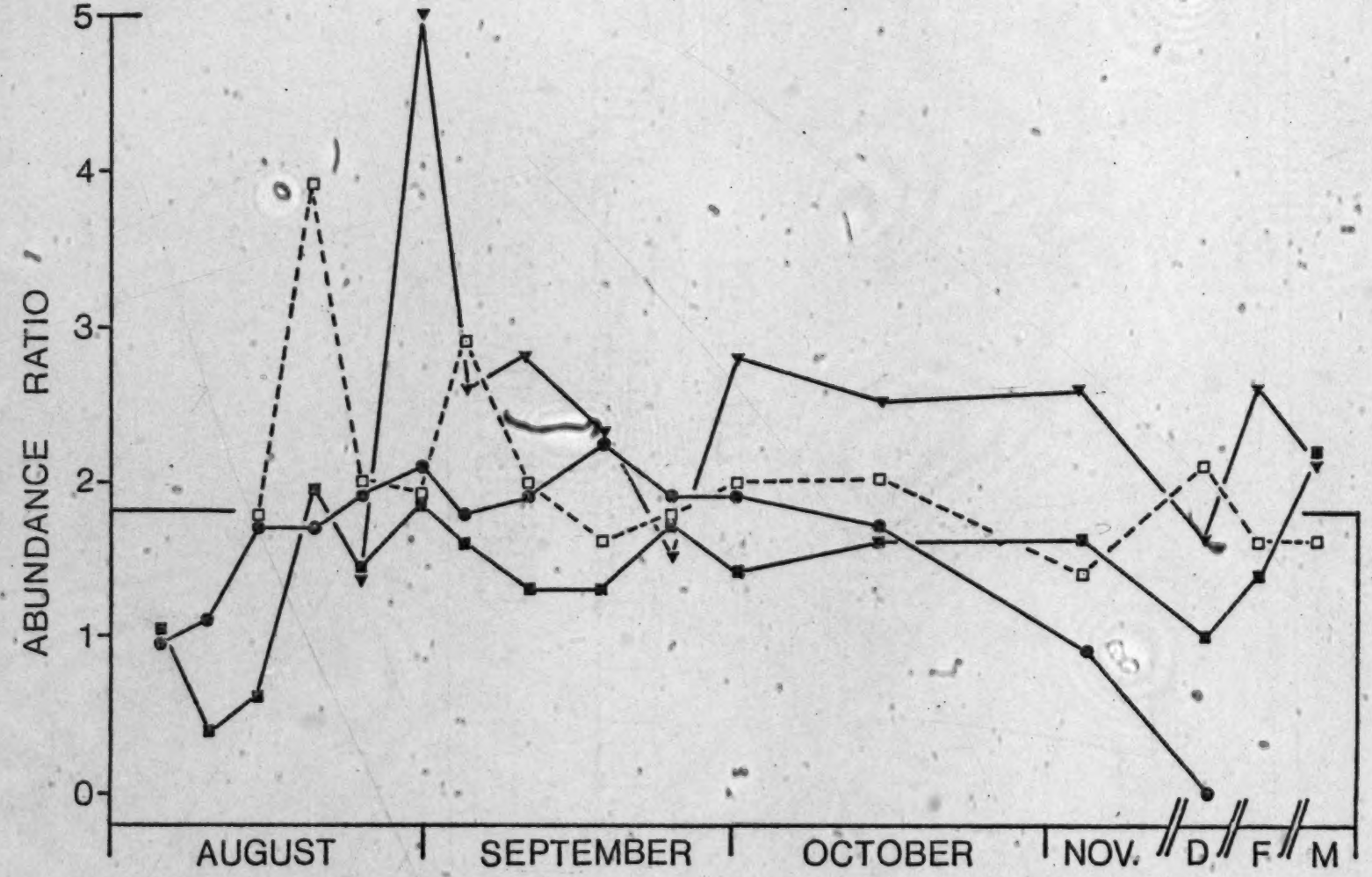


Fig. 28. Change in the proportion of larvae of G. tobiferus to those of G. nr. paripes (= abundance ratio) in each instar in the dead plant shoots during the two species' 1973-74 cohort. Instar I (●); Instar II (■); Instar III (□); Instar IV (▼). The horizontal line at 1.8 represents the abundance ratio based on the estimated number of eggs deposited per square meter to start each cohort. D, F and M represent December, February and May.


ABUNDANCE RATIO
5
4
3
2
1
0
AUGUST
SEPTEMBER
OCTOBER
NOV.
D
F
M

short days in all cases could be reversed by long days. All dormant larvae moved and consumed food.

Temperature also was involved. In the C. nuditarsis population short days only accompanied by a low temperature could induce dormancy.

In all three populations studied, the type of dormancy induced by short days was oligopause[6].

If dormancy did occur in the G. lobiferus population, then it would appear that at least some of the fourth instar larvae entered the dormancy phase in spring under the stimulus of longer days, and possibly also some did so the preceding fall, in response to the shorter days. Temperature may have acted in conjunction with photoperiod to produce the dormancy.

Thus it would appear that in addition to being a superior competitor, G. lobiferus uses environmental cues to stagger its time of emergence, thereby minimizing the chance of all the adults (and hence the progeny) being killed due to a sudden change in the weather conditions.

In conclusion, the results obtained in the present study may be regarded only as a small contribution to the development of a predictive model of the dynamics of natural populations of chironomids. Previous work on this family suggests that the generalized survivorship

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[6]Oligopause is a type of dormancy which is facultative and is similar to quiescence. It differs from it in that the halting of development does not immediately follow the deterioration of the environmental factors, but only with a retardation. The new start of the development after a change of environment to optimal conditions also is retarded (Müller, 1970).

curve is representative of many species. Thus it should be of value also in other studies, e.g. in calculating turnover rates for productivity estimates (cf. Waters, 1969).

Several assumptions have been made in the development of the life tables, principal among which is that each female which survives lays only one egg mass. Since all assumptions made have been detailed, subsequent results can be applied to refine the estimates.

The results obtained suggest the competitive superiority of G. lobiferus in a pure Typha marsh. Since T. latifolia is world wide in distribution, it would be of interest to check the above conclusion in other geographical localities, and hence determine limiting factors.

REFERENCES

Biever, K.D. 1967. Biological studies on chironomids with emphasis on the temperature relations of the developmental stages. Ph.D. Thesis, U. of California, Riverside, 111pp.

Brinkhurst, R.O. 1967. Sampling the benthos. Great Lakes Inst., Progr. Rept. 32, Univ. of Toronto, 7pp.

Burtt, E.T. 1940. A filter-feeding mechanism in a larva of the Chironomidae (Diptera: Nematocera). Proc. Roy. ent. Soc. Lond., Ser. A, 15: 113.

Cooper, W.E. 1965. Dynamics and production of a natural population of a freshwater amphipod, Hyalella azteca. Ecol. Monogr., 35: 377-394.

Dublin, L.I., and Lotka, A.J. 1925. On the true rate of increase as exemplified by the population of the United States, 1920. J. Amer. Statist., Ser. A, 20: 305-339.

Elliott, J.M. 1971. Some methods for the statistical analyses of samples of benthic invertebrates. Freshwater Biological Association, Sci. Publ. No. 25, 144pp.

Elliott, J.M. 1973. The life cycle and production of the leech Erpobdella octoculata. J. Anim. Ecol. 42:

Fischer, J. 1974. Experimentelle Beiträge zur Ökologie von Chironomus (Diptera). I. Dormanz bei Chironomus nuditarsis und Ch. plumosus. Oecologia, 16: 73-95.

Hall, D.J. 1964. An experimental approach to the dynamics of a natural population of Daphnia galeata mendotae. Ecology, 45: 94-112.

Hamilton, A.L., Saether, O.A., and Oliver, D.R. 1969. A classification of the Nearctic Chironomidae (Diptera). F.R.B.C. Tech. Rept., No. 124, 42pp.

Hamilton, A.L., Saether, O.A., and Oliver, D.R. In Prep. A handbook of the Canadian Chironomidae (Diptera).

Hunter, D.K. 1965. Gurleya sp., a microsporidian parasite of Chironomus (= Dicrotendipes) californicus Johannsen. M. Sc. Thesis, U. of California, Riverside, 54pp.

Hutchinson, G.E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals. Amer. Nat., 93: 145-159.

Itô, Y. 1959. A comparative study of survivorship curves for natural insect populations. Jap. J. Ecol., 9: 107-115.

Itô, Y. 1961. Factors that affect the fluctuations of animal numbers, with special reference to insect outbreaks. Bull. Nat. Inst. Agric. Sci., Ser. C, No. 13, pp. 57-89.

Kajak, Z. 1965. Chwytacz rurowy do probieran prob dna. Ekol. Polska, Ser. B, 11: 159-165.

Leathers, A.L. 1922. Ecological study of aquatic midges and some related insects with special reference to feeding habits. Bull. U.S. Bur. Fisheries, 38: 1-62.

MacArthur, R.H., and Wilson, E.G. 1967. The Theory of Island Biogeography. Princeton University Press, 203pp.

Mann, K.H. 1957. A study of a population of the leech Glossiphonia complanata (L.). J. Anim. Ecol., 26: 99-111.

McCauley, V.J.E. 1974. Instar differentiation in larval Chironomidae (Diptera). Can. Ent., 106: 179-200.

Müller, H.J. 1970. Formen der Dormanz bei Insekten. Nova Acta Leopoldina, 35: 1-27.

Mundie, J.H. 1957. The ecology of Chironomidae in storage-reservoirs. Trans. Roy. ent. Soc. Lond. Ser. A, 109: 149-232.

Nielsen, E.T. 1962. Contributions to the ethology of Glyptotendipes (Phytotendipes) paripes (Edwards). Oikos, 13: 48-75.

Pianka, E.R. 1974. Evolutionary Ecology. Harper and Row, 356pp.

Price, P.W. 1972. Parasitoids utilizing the same host: adaptive nature of differences in size and form. Ecology, 53: 190-195.

Schiff, D. J. 1964. Studies on Bulinus (Physopsis) globosus in Rhodesia. I. The influence of temperature on the intrinsic rate of natural increase. Ann. Trop. Med. Parasitol., 58: 94-105.

Schiff, C.J., and Garnett, B. 1967. The influence of temperature on the intrinsic rate of natural increase of the freshwater snail Biomphalaria pfeifferi (Kraus) (Pulmonata: Planorbidae). Arch. Hydrobiol., 62: 429-438.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science, 85: 27-39.

Slobodkin, L.B. 1963. Growth and Regulation of Animal Populations. Holt, Reinhart and Winston, 183pp.

Stiven, A.E. 1962. The effect of temperature and feeding on the intrinsic rate of increase of three species of Hydra. Ecology 43: 325-328.

Sturrock, R.F. 1966. The influence of temperature on the biology of Biomphalaria pfeifferi (Krauss), an intermediate host of Schistosoma mansoni. Ann. Trop. Med. Parasitol., 60: 100-105.

Sturrock, R.F., and Sturrock, B.M. 1972. The influence of temperature on the biology of Biomphalaria glabrata (Say), intermediate host of Schistosoma mansoni on St. Lucia, West Indies. Ann. Trop. Med. Parasitol. 66: 385-390.

Thiele, H.U. 1971. Die Steuerung der Jahresrhythmik von Carabiden durch exogene und endogene Faktoren. Zool. Jb. Syst., 98: 341-371.

Thienemann, A. 1954. Chironomus. Leben, Verbreitung und wirtschaftliche Bedeutung der Chironomiden. Binnengewasser, 20: 1-834.

Walshe, B.M. 1951. The feeding habits of certain Chironomid larvae (subfamily Tendipedinae). Proc. Zool. Soc. Lond., 121: 63-79.

Waters, T.F. 1969. The turnover ratio in production ecology of freshwater invertebrates. Amer. Nat., 103: 173-185.

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APPENDIX I

MORPHOLOGICAL DIFFERENTIATION OF GLYPTOTENDIPES DREISBACHI, GLYPTOTENDIPES LOBIFERUS AND GLYPTOTENDIPES NR. PARIPES.

INTRODUCTION

Glyptotendipes dreisbachi, G. lobiferus and G. nr. paripes[1], especially the latter two species, exhibit pronounced morphological similarities in most developmental stages. As a basic requisite for the construction of a life table for each is the accurate differentiation of each in all developmental stages, a detailed examination was made of the three species to determine criteria suitable for their separation.

G. lobiferus posed additional problems. Its developmental pattern in George Lake is such that for part of each year larvae, pupae and adults from two consecutive generations occur together. These have been examined to determine methods suitable for their separation.

EGG

The eggs of G. dreisbachi are lime green in color whereas those of the other two species are light golden brown. Similar to G. dreisbachi, the eggs of G. nr. paripes do not exhibit any fixed pattern of distribution within the egg mass, whereas those of G. lobiferus do. Its egg mass consists of a single strand of eggs which forms a series of U-shaped loops, the tops of each U doubling back on themselves. The long axis of all eggs are parallel and point into the center of the cylinder of jelly.

Although the egg mass of each species is sausage-shaped, they

[1] This may be a new species, intermediate between Glyptotendipes paripes Edwards and Glyptotendipes meridionalis Dendy and Sublette (Pers. Comm., Dr. D.M. Webb, Illinois Natural History Survey, University of Illinois, Urbana, Illinois).

differ in size, and in the number and size of the eggs (Table 1).

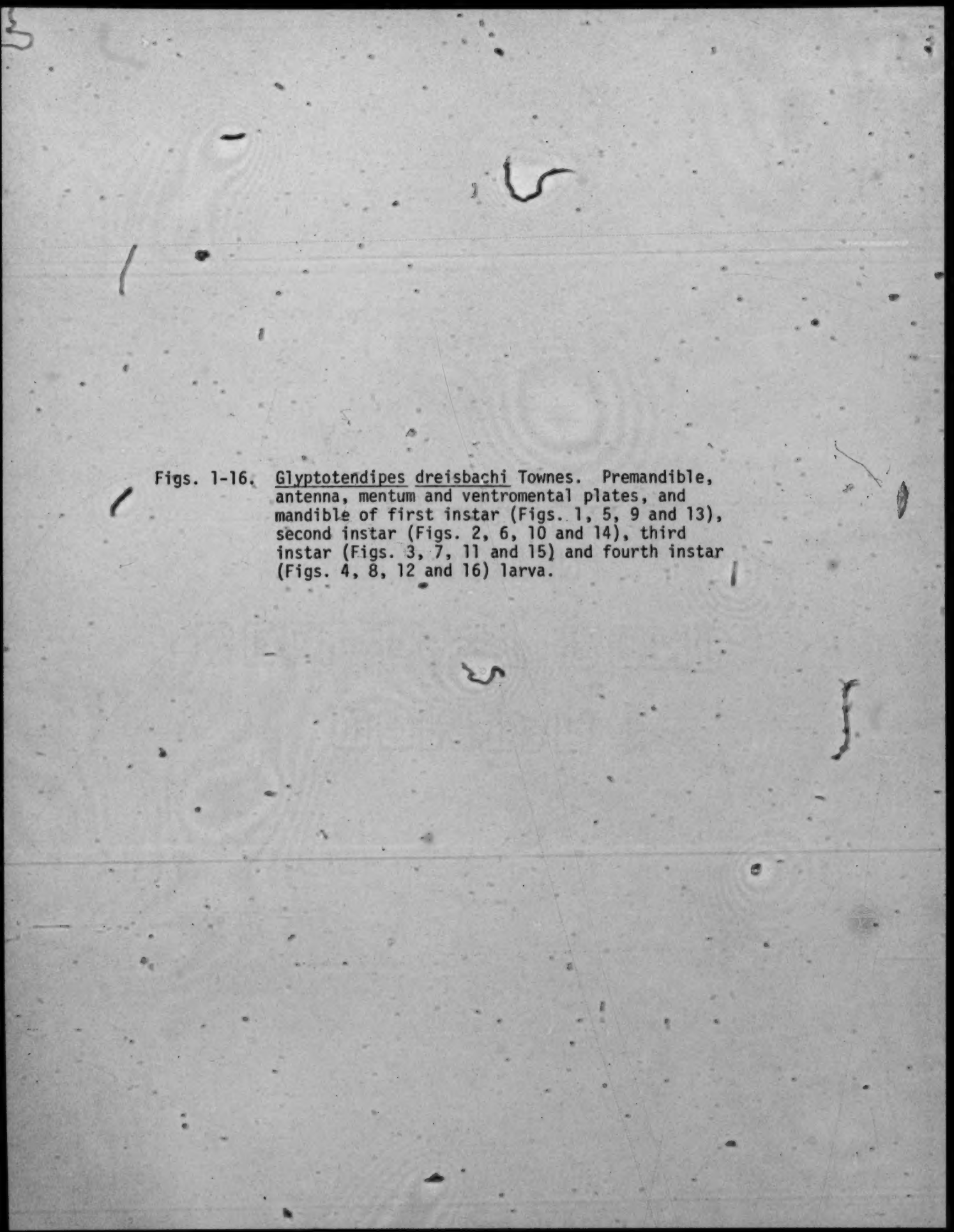
LARVA

Examination of the antennae, premandibles, mandibles, and mentum and associated ventromental plates of each of the four instars of each of the three species (Figs. 1-48) shows that G. dreisbachi can be separated from the other two species in instars II, III, and IV simply by visual examination of the patterning of the teeth on the mentum. In instar I however, measurements must be made. Comparison of the length of the mandibles, the width of the mentum, the distance from the apex of the mentum to the posterior edge of the head capsule (Figs. 49-51), the length of each of the antennal flagellomeres, and the length and breadth of the head capsule of the three species shows that the length of the second antennal flagellomere is the best single measurement for separating instar I larvae of G. dreisbachi from those of G. lobiferus and G. nr. paripes (Tables 2, 3, and 4); however, only slightly more than 95% of the specimens can be separated accurately. When this measurement is taken in conjunction with one or more of the other measurements, such as the length of the first and third antennal flagellomeres, then the accuracy of separation is increased.

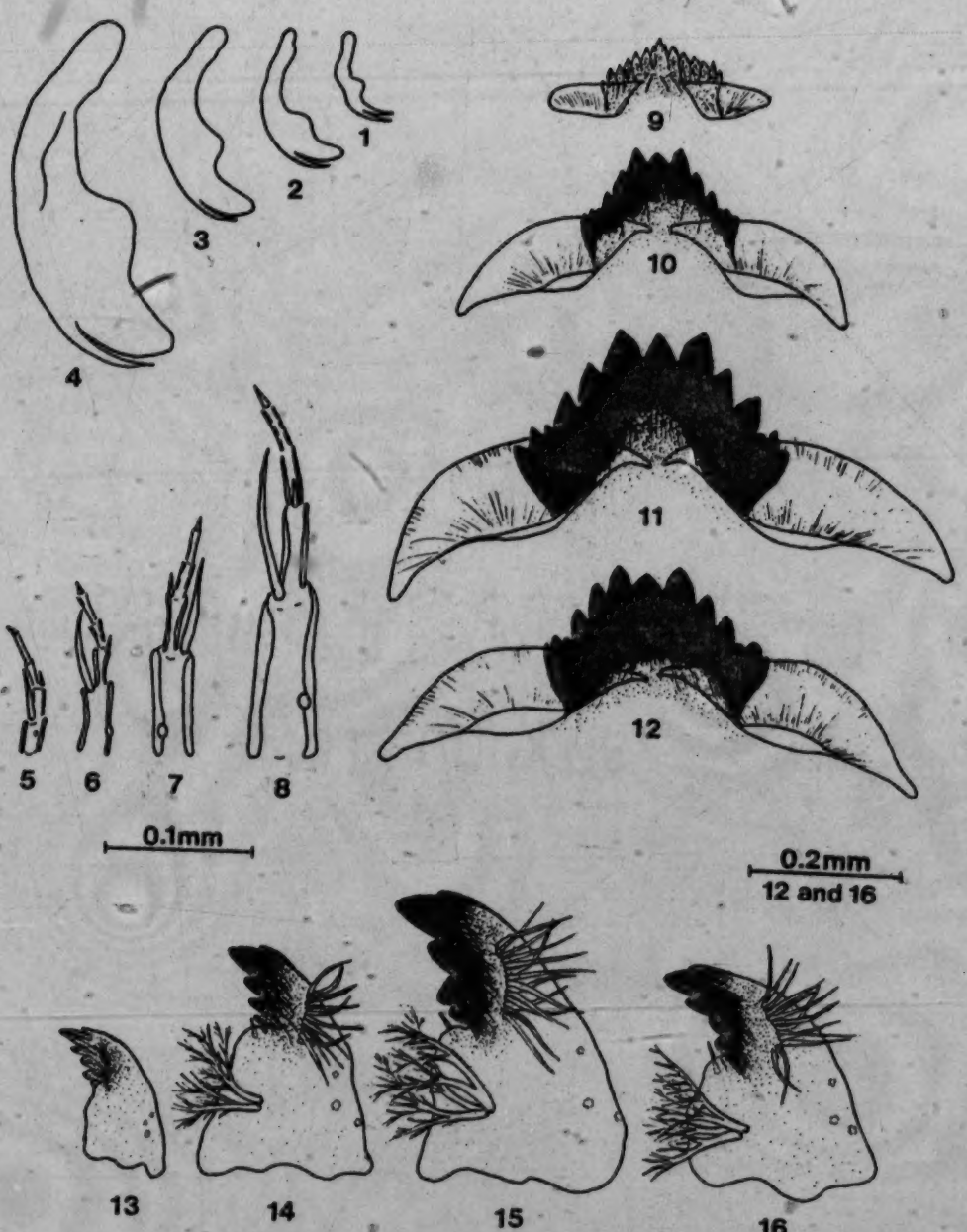
G. lobiferus and G. nr. paripes can be separated from each other completely only in instars II, III and IV, and only by measurement of the distance from the apex of the mentum to the posterior ventral edge of the head capsule (Tables 3, 4 and 5).

Table 1. Comparison of size of egg mass (mm.), number of eggs per egg mass, and size of eggs (u) of the three species of Glyptotendipes. The data for G. lobiferus and G. nr. paripes are based on egg masses collected throughout the summer, while those for G. dreisbachi are based solely on egg masses collected in the spring.

Species		Egg Mass			Egg	
		Length	Width	No. of Eggs	Length	Width
G. dreisbachi	Mean	13.0	5.9	519.4	356	120
	Range	6.8 - 22.5	5.2 - 6.8	424 - 675	350 - 370	110 - 130
	No. Examined	6	5	8	9	9
G. lobiferus	Mean	10.9	2.6	1313.2	392	116
	Range	8.6 - 14.7	2.3 - 3.3	995 - 1800	380 - 400	110 - 120
	No. Examined	6	6	17	10	10
G. nr. paripes	Mean	11.5	5.4	1007.7	338	108
	Range	7.9 - 16.0	4.1 - 7.2	745 - 1379	330 - 340	100 - 110
	No. Examined	7	6	13	8	8



Figs. 1-16. Glyptotendipes dreisbachi Townes. Premandible, antenna, mentum and ventromental plates, and mandible of first instar (Figs. 1, 5, 9 and 13), second instar (Figs. 2, 6, 10 and 14), third instar (Figs. 3, 7, 11 and 15) and fourth instar (Figs. 4, 8, 12 and 16) larva.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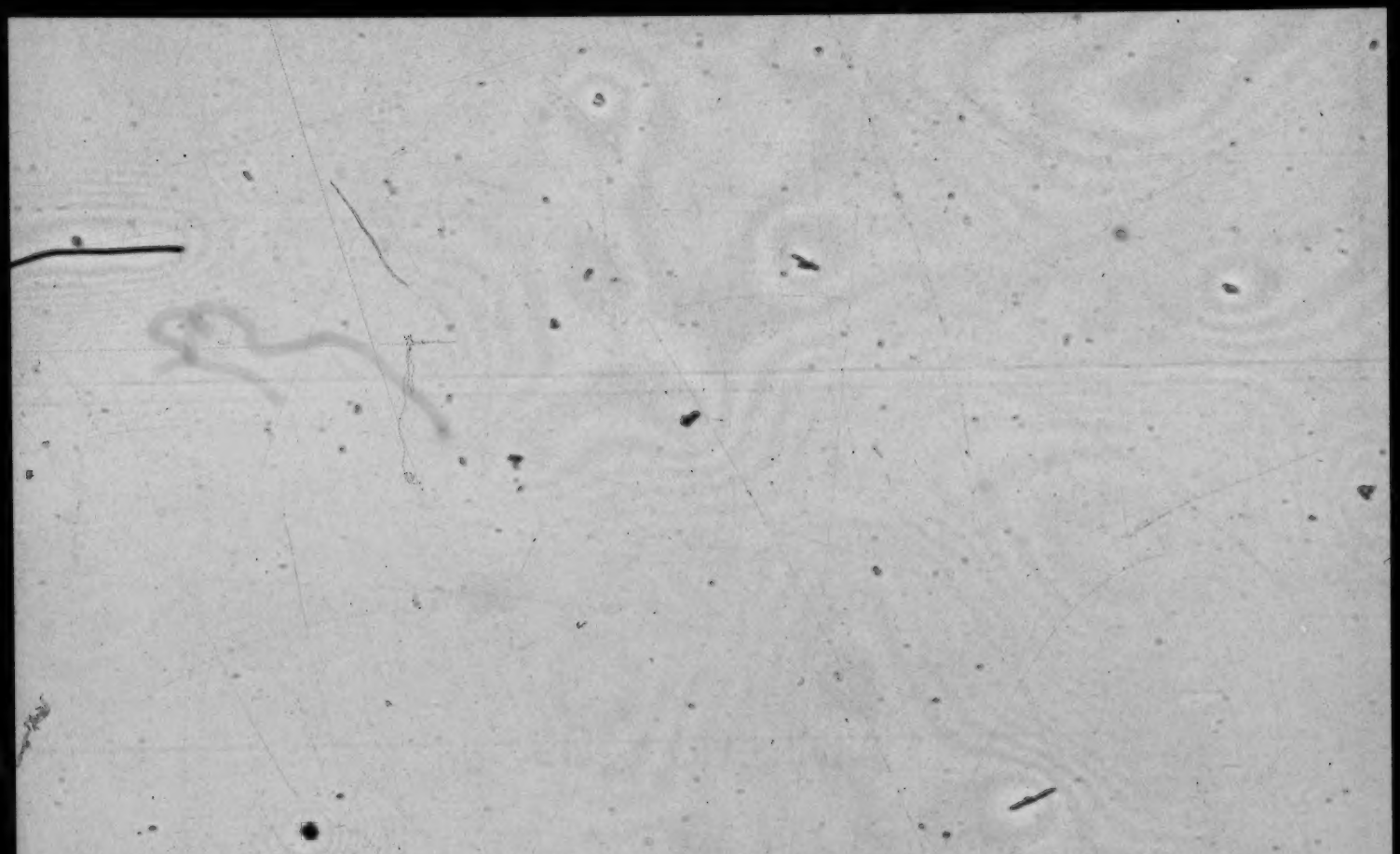
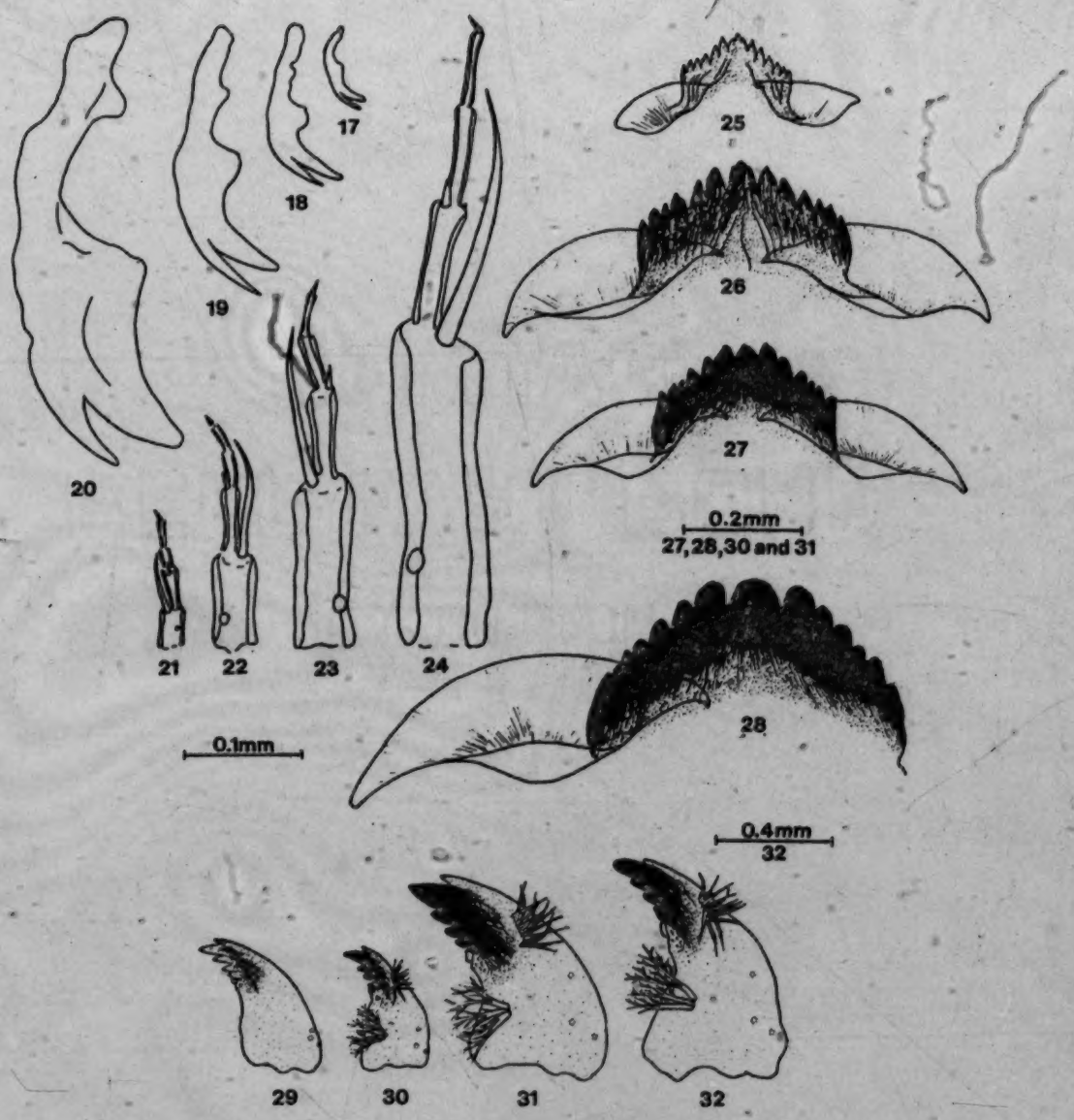


Figs. 17-32. Glyptotendipes lobiferus (Say). Premandible, antenna, mentum and ventromental plates, and mandible of first instar (Figs. 17, 21, 25 and 29), second instar (Figs. 18, 22, 26 and 30), third instar (Figs. 19, 23, 27 and 31) and fourth instar (Figs. 20, 24, 28 and 32) larva.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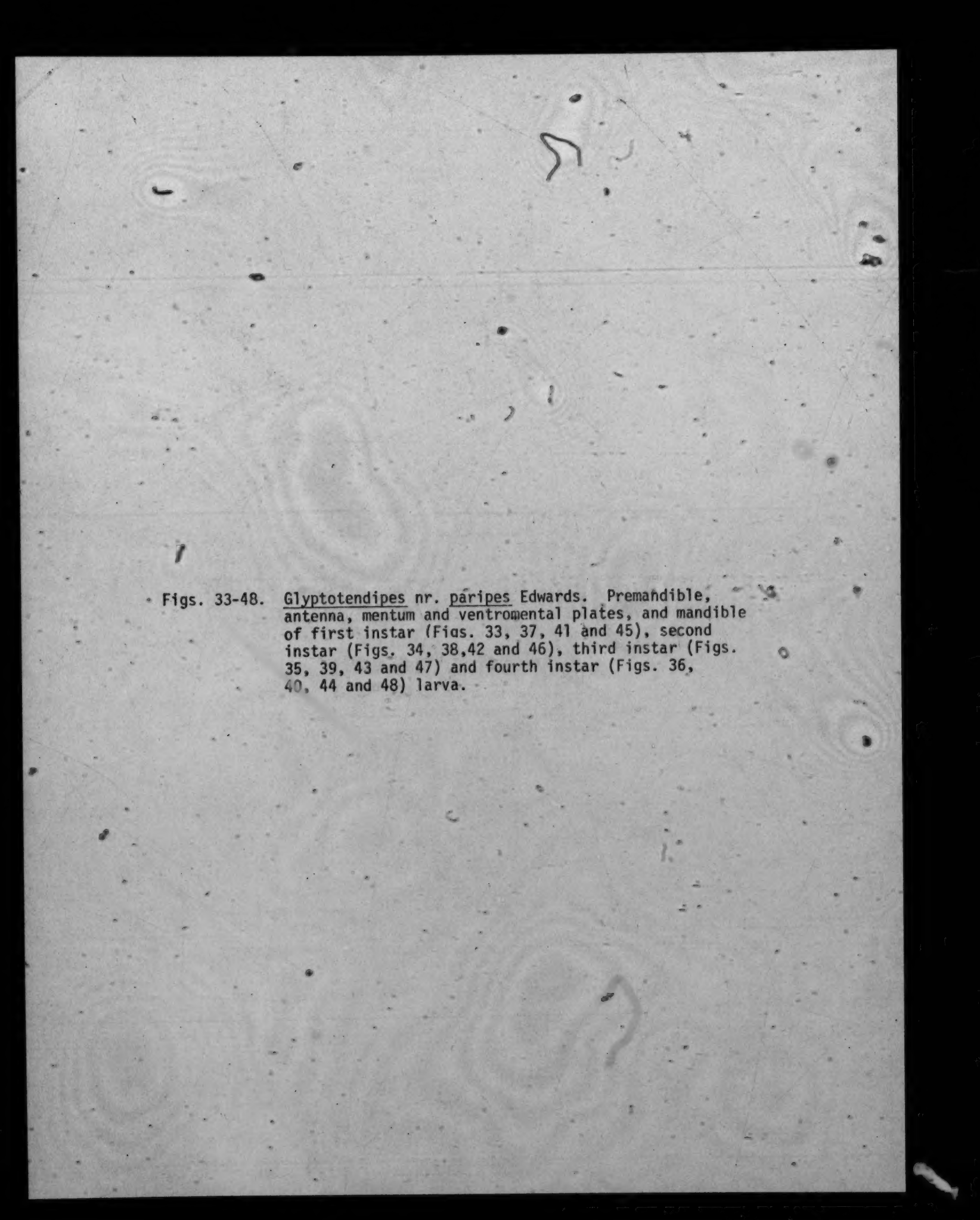
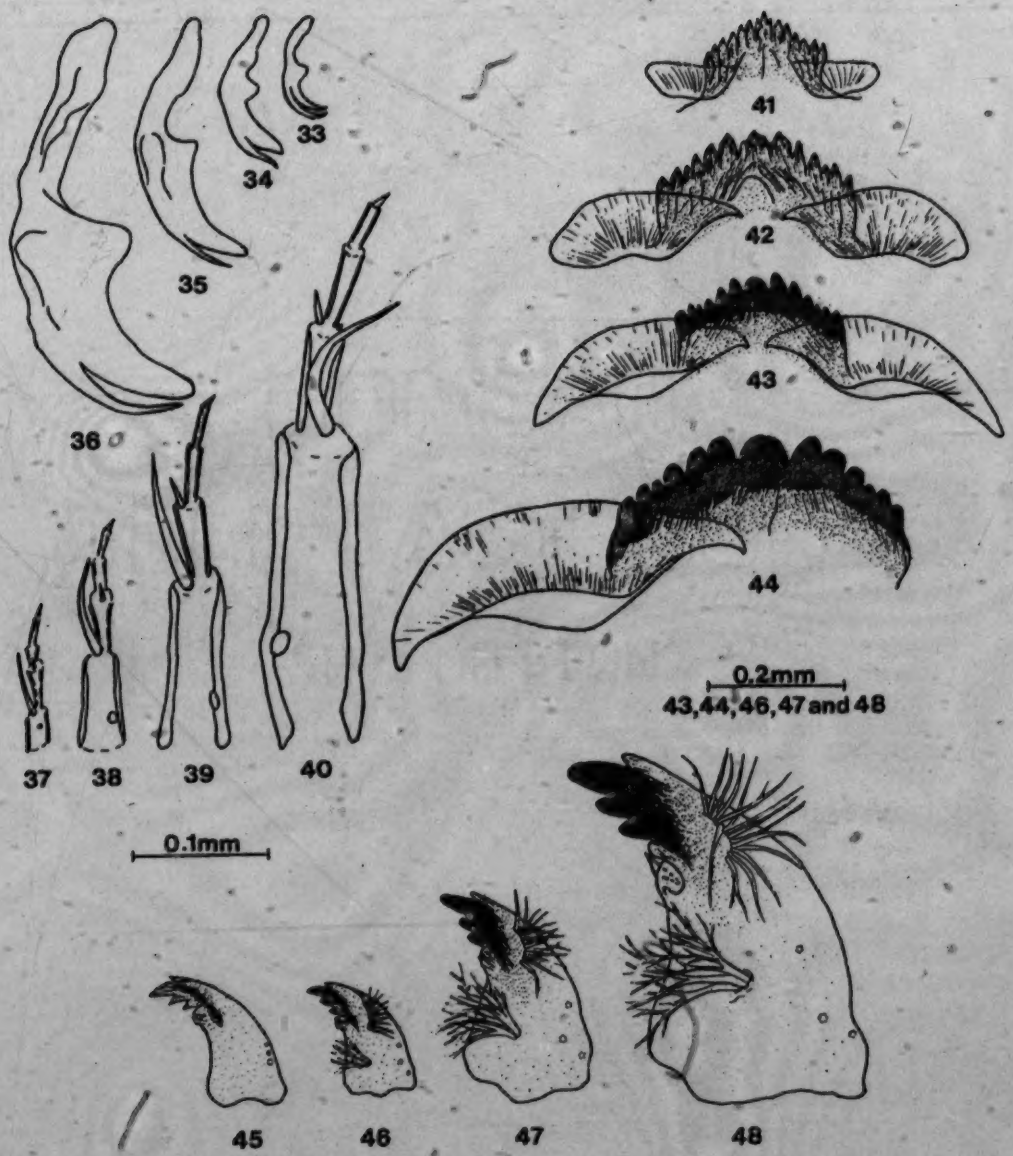


Figs. 33-48. Glyptotendipes nr. paripes Edwards. Premandible, antenna, mentum and ventromental plates, and mandible of first instar (Figs. 33, 37, 41 and 45), second instar (Figs. 34, 38,42 and 46), third instar (Figs. 35, 39, 43 and 47) and fourth instar (Figs. 36, 40, 44 and 48) larva.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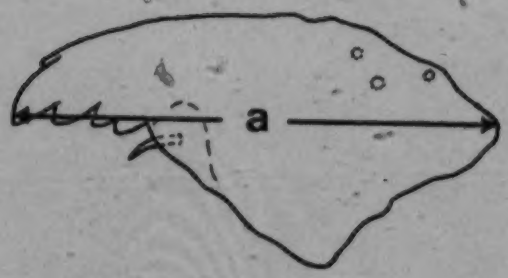
Figs 49-51. Three of the measurements made on each of the four larval instars to differentiate the three species of Glyptotendipes. Fig. 49 : length of mandible (a); Fig. 50 : width of mentum (b); Fig. 51 : distance from apex of mentum to the posterior ventral edge of the head capsule, in the mid line (c).



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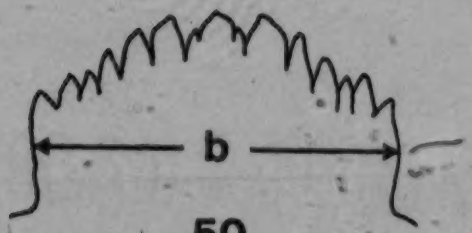

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Table 2. Comparison of the length of the antennal flagellomeres, length of the mandibles (a), width of the mentum (b), and the distance from the apex of the mentum to the posterior ventral edge of the head capsule (c) of the four instars of G. dreisbachi. All measurements in microns.

Instar		Length of Antennal Flagellomere					Length		
		I	II	III	IV	V	a	b	c
I	Mean ± 2SD	10 ± 1	11 ± 1	6 ± 1	10 ± 2	3 ± 1	56 ± 4	37 ± 3	69 ± 4
	Range	8 - 11	10 - 13	5 - 6	9 - 12	2 - 4	52 - 61	35 - 39	65 - 73
	No. Measured	52	54	52	52	50	55	53	49
II	Mean ± 2SD	24 ± 2	12 ± 0	9 ± 1	10 ± 1	4 ± 0	82 ± 7	53 ± 6	114 ± 10
	Range	20 - 25	11 - 13	7 - 10	8 - 12	4 - 5	75 - 90	49 - 58	107 - 122
	No. Measured	6	6	6	6	6	20	16	15
III	Mean ± 2SD	35 ± 2	16 ± 1	10 ± 1	13 ± 0	4 ± 1	129 ± 11	94 ± 14	179 ± 13
	Range	31 - 38	14 - 18	8 - 11	12 - 14	3 - 5	110 - 139	81 - 107	165 - 186
	No. Measured	6	6	6	6	6	34	30	32
IV	Mean ± 2SD	72 ± 10	23 ± 2	16 ± 1	17 ± 1	6 ± 0	195 ± 37	154 ± 21	282 ± 45
	Range	64 - 81	19 - 26	14 - 17	14 - 17	4 - 6	177 - 232	145 - 180	255 - 319
	No. Measured	10	9	9	9	9	11	11	10

Table 3. Comparison of the length of the antennal flagellomeres, length of mandibles (a), the width of the mentum (b), and the distance from the apex of the mentum to the posterior ventral edge of the head capsule (c) of the four instars of G. lobiferus. All measurements in microns.

Instar		Length of Antennal Flagellomere					Length		
		I	II	III	IV	V	a	b	c
I	Mean ± 2SD	13 ± 2	16 ± 3	7 ± 1	10 ± 2	3 ± 1	61 ± 6	42 ± 4	78 ± 12
	Range	11 - 15	13 - 18	7 - 8	9 - 13	2 - 4	55 - 67	39 - 45	71 - 90
	No. Measured	87	88	93	84	79	89	84	60
II	Mean ± 2SD	38 ± 3	20 ± 3	14 ± 3	13 ± 2	4 ± 1	127 ± 12	76 ± 7	164 ± 10
	Range	35 - 40	17 - 23	11 - 16	12 - 15	4 - 5	116 - 133	70 - 81	155 - 174
	No. Measured	59	50	47	47	48	49	45	45
III	Mean ± 2SD	74 ± 8	33 ± 6	24 ± 4	19 ± 3	5 ± 1	243 ± 29	162 ± 15	310 ± 24
	Range	62 - 80	26 - 38	19 - 26	16 - 21	5 - 6	203 - 264	148 - 162	264 - 322
	No. Measured	35	35	30	33	31	31	35	35
IV	Mean ± 2SD	135 ± 30	41 ± 10	31 ± 9	24 ± 5	7 ± 1	367 ± 74	241 ± 61	479 ± 72
	Range	108 - 167	35 - 55	25 - 43	20 - 30	6 - 8	296 - 454	200 - 328	412 - 551
	No. Measured	67	63	58	56	54	67	63	68

Table 4. Comparison of the length of the antennal flagellomeres, length of the mandibles (a), the width of the mentum (b), and the distance from the apex of the mentum to the posterior ventral edge of the head capsule (c) of the four instars of G. nr. paripes. All measurements in microns.

Instar		Length of Antennal Flagellomere					Length		
		I	II	III	IV	V	a	b	c
I	Mean ± 2SD	12 ± 2	16 ± 3	8 ± 1	10 ± 2	3 ± 1	61 ± 7	41 ± 5	72 ± 8
	Range	10 - 14	13 - 19	7 - 9	8 - 12	2 - 4	55 - 69	36 - 46	62 - 78
	No. Measured	93	94	88	80	75	93	80	80
II	Mean ± 2SD	35 ± 4	20 ± 3	13 ± 2	12 ± 2	4 ± 1	112 ± 13	74 ± 10	134 ± 12
	Range	30 - 39	17 - 24	11 - 16	10 - 13	4 - 6	102 - 125	67 - 83	122 - 145
	No. Measured	71	70	67	68	67	70	62	64
III	Mean ± 2SD	66 ± 6	30 ± 4	22 ± 4	16 ± 3	5 ± 1	201 ± 23	136 ± 18	228 ± 25
	Range	62 - 73	26 - 35	19 - 24	14 - 19	5 - 6	180 - 229	125 - 154	203 - 252
	No. Measured	50	45	38	43	31	45	49	47
IV	Mean ± 2SD	122 ± 14	39 ± 7	29 ± 5	21 ± 3	7 ± 1	338 ± 23	225 ± 18	365 ± 20
	Range	106 - 136	30 - 43	26 - 33	19 - 22	7 - 8	325 - 354	215 - 244	354 - 383
	No. Measured	14	12	11	11	11	12	13	17

Table 5. Comparison of the length and breadth of the head capsule of each of the four larval instars of the three species of Glyptotendipes. All values in mm.

Species	Instar	Number Measured	Head Capsule Length				Head Capsule Width			
			Minimum	Maximum	Mean	± 2SD	Minimum	Maximum	Mean	± 2SD
G. dreisbachi	I	75	0.13	0.18	0.16	0.02	0.09	0.14	0.12	0.02
	II	150	0.20	0.26	0.23	0.03	0.15	0.19	0.17	0.02
	III	149	0.30	0.40	0.35	0.04	0.23	0.28	0.25	0.03
	IV	149	0.50	0.66	0.56	0.08	0.33	0.46	0.39	0.06
G. lobiferus	I	93	0.15	0.20	0.17	0.02	0.11	0.16	0.13	0.02
	II	105	0.30	0.39	0.35	0.03	0.21	0.27	0.24	0.02
	III	148	0.53	0.72	0.63	0.08	0.36	0.46	0.42	0.04
	IV	239	0.91	1.26	1.08	0.15	0.62	0.86	0.74	0.12
G. nr. paripes	I	172	0.14	0.18	0.16	0.02	0.10	0.14	0.12	0.01
	II	108	0.25	0.34	0.30	0.04	0.19	0.24	0.22	0.03
	III	179	0.43	0.57	0.51	0.06	0.34	0.42	0.37	0.04
	IV	205	0.74	0.92	0.83	0.08	0.56	0.69	0.63	0.06

Only limited accuracy can be obtained in separating G. lobiferus and G. nr. paripes in instar I. Of the measurements made, the distance from the apex of the mentum to the posterior ventral edge of the head capsule, and the length of the head capsule are the most useful. As the frequency distributions of each species for each of these two measurements were found to be normal, those larvae which fall in that part of each distribution common to both species can be divided in a ratio based on the number of specimens of each species which can be separated accurately.

PUPA

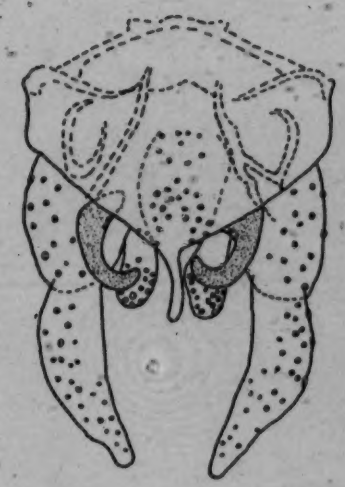
All three species possess sclerotized structures in the shape of maces located on some of the tergites. In G. dreisbachi there are four maces, located on tergites III-VI, whereas in G. lobiferus and in G. nr. paripes there are five maces, located on tergites II-VI (Figs. 55-68).

The pupa of G. lobiferus differs from that of G. nr. paripes in that the dorsal surface of the maces on tergites V and VI of the former species is covered with many small spines, whereas that of G. nr. paripes always is devoid of such spines (Figs. 62, 63, 67 and 68).

ADULT

The usual method for differentiating chironomid male adults is according to the structure of the hypopygium. This method cannot be used for separating G. dreisbachi, G. lobiferus and G. nr paripes (Figs. 52, 53 and 54).

Figs. 52-68. Hypopygium of Glyptotendipes dreisbachi (Fig. 52), G. lobiferus (Fig. 53) and G. nr. paripes (Fig. 54). Maces on pupal tergites III-VI of G. dreisbachi (Figs. 55-58), on tergites II-VI of G. lobiferus (Figs. 59-63) and on tergites II-VI of G. nr. paripes (Figs. 64-68).



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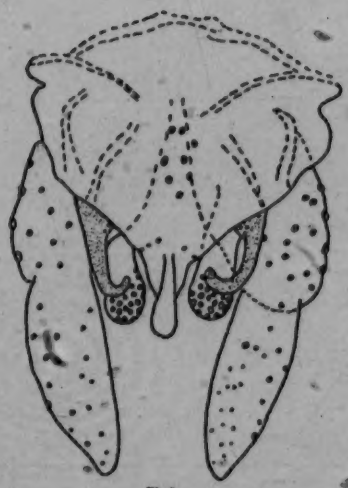

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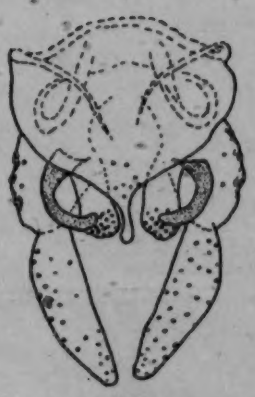

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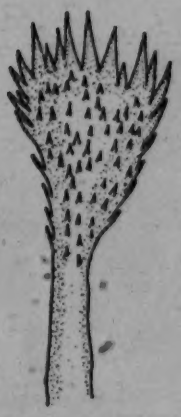

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Comparison of the antennal ratio (A.R.), the number of setae on the clypeus, the length of the segments of the palpi (Table 6), the number of various types of setae on the thorax and certain wing measurements (Table 8) of the three species indicates that all male G. dreisbachi can be separated from those of G. lobiferus and G. nr. paripes according to the number of setae on the scutellum. Of these criteria, only the number of acrostichals can be used to separate all G. lobiferus from G. nr. paripes.

Comparison of the lengths of various leg segments and associated ratios (Tables 9, 10 and 11) of the three species shows that all male G. dreisbachi can be separated from those of the other two species by the leg ratio (L.R.) and by the ratio Ta_2/Ta_3. Of these criteria, only the length of the second tarsal segment can be used to separate all G. lobiferus from G. nr. paripes.

Comparison of the various measurements of the female adults of the three species (Tables 6-11) indicates that all three species can be separated completely from each other by the length of the third antennal flagellomere (Table 7), and by the number of setae on the scutellum (Table 8).

Table 6. Comparison of the number of setae on the clypeus and the palp lengths of the males and of the females, and the antennal ratio of the males, of the three species of Glyptotendipes. Means and ranges given.

Species	Sex	Number Measured	Antennal Ratio	No. of Setae on Clypeus	Palp Lengths (μ)			
					I	II	III	IV
G. dreisbachi	M	4	3.32 3.21 - 3.54	27.5 21 - 30	64 61 - 67	173 162 - 190	179 168 - 197	239 225 - 260
G. lobiferus	M	15	3.93 3.34 - 3.47	42.5 27 - 56	78 68 - 88	239 187 - 274	229 180 - 273	326 239 - 390
G. nr. paripes	M	6	3.78 3.24 - 4.17	33.5 30 - 38	69 65 - 77	214 197 - 246	207 191 - 215	255 220 - 274
G. dreisbachi	F	5		30.0 25 - 35	60 51 - 68	159 138 - 183	177 157 - 193	224 199 - 255
G. lobiferus	F	5		56.8 46 - 66	74 61 - 77	214 174 - 262	207 174 - 236	300 225 - 387
G. nr. paripes	F	2		32.5 32 - 33	63 62 - 64	194 183 - 206	206 203 - 210	274 258 - 290

Table 7. Comparison of the lengths of the antennal flagellomeres of the female adults of the three species of Glyptotendipes. Means and ranges given.

Species	Number Measured	Length of Flagellomere (μ)					
		II	III	IV	V	VI	VII
G. dreisbachi	5	88 81 - 96	81 72 - 87	94 87 - 107	96 87 - 107	108 96 - 119	220 154 - 229
G. lobiferus	5	122 107 - 143	111 95 - 137	131 113 - 161	134 113 - 167	137 119 - 161	284 238 - 387
G. nr. paripes	2	98 96 - 100	90 88 - 93	110 107 - 112	112 104 - 119	107 99 - 116	197 170 - 223

Table 8. Comparison of the number of various types of setae on the thorax and certain wing measurements of the males and the females of the three species of Glyptotendipes. Wing length in mm.

Species	Sex	Number Measured	Setae on Thorax					Wing		
			Acro-stichals	Dorso-centrals	Noto-pleurals	Supra-alars	Scutellars	Length	V.R.	No. of hairs on Squama
G. dreisbachi	M	4	24.7 24 - 26	25.3 20 - 30	7.8 6 - 11	1.2 1 - 2	22.8 20 - 25	3.32 2.98 - 3.63	1.02 1.00 - 1.04	26.9 22 - 31
G. lobiferus	M	15	29.0 25 - 35	37.4 28 - 57	10.6 8 - 14	1.5 1 - 3	45.9 33 - 58	3.78 3.21 - 4.70	1.03 1.00 - 1.07	26.2 19 - 35
G. nr. paripes	M	6	19.5 17 - 23	26.6 17 - 35	6.8 5 - 8	1.0 0 - 1	36.2 30 - 44	3.47 3.12 - 3.92	1.05 1.02 - 1.06	19.3 15 - 25
G. dreisbachi	F	5	23.8 21 - 28	25.5 19 - 36	7.5 6 - 10	1.0 1	21.6 19 - 29	3.48 2.84 - 4.33	1.12 1.09 - 1.14	27.4 19 - 34
G. lobiferus	F	5	32.8 30 - 35	46.6 37 - 58	11.0 8 - 13	2.0 0 - 4	55.4 48 - 74	4.65 4.30 - 5.26	1.09 1.06 - 1.13	41.2 27 - 69
G. nr. paripes	F	2	24.0 23 - 25	35.0 32 - 40	6.5 6 - 7	1.0 1	37.0 35 - 39	3.50 3.28 - 3.72	1.09 1.08 - 1.10	21.8 19 - 25

Table 9. Lengths and proportions of legs for four male and five female G. dreisbachi. Ranges and means in mm.

	Sex	Fe	Ti	Ta_1	Ta_2	Ta_3	Ta_4	Ta_5	L.R.	Ta_2/Ti	Ta_2/Ta_3
P_1	M	1.18 1.14-1.22	1.19 1.16-1.22	1.47 1.40-1.54	0.62 0.58-0.64	0.66 0.62-0.70	0.56 0.54-0.58	0.24 0.18-0.26	1.24 1.22-1.28	0.52 0.50-0.53	0.93 0.91-0.94
	F	1.10 0.94-1.16	1.13 0.92-1.44	1.46 1.30-1.70	0.56 0.50-0.68	0.54 0.48-0.68	0.43 0.38-0.50	0.23 0.20-0.28	1.33 1.17-1.43	0.49 0.47-0.54	1.02 1.00-1.04
P_2	M	1.29 1.24-1.36	1.31 1.16-1.40	0.62 0.54-0.66	0.40 0.36-0.42	0.34 0.30-0.36	0.24 0.22-0.24	0.17 0.16-0.18	0.47 0.46-0.49	0.30 0.30-0.31	1.18 1.17-1.20
	F	1.28 1.10-1.62	1.37 1.14-1.70	0.62 0.54-0.78	0.38 0.34-0.46	0.30 0.22-0.40	0.22 0.18-0.28	0.17 0.14-0.22	0.46 0.44-0.47	0.27 0.26-0.30	1.23 1.15-1.54
P_3	M	1.43 1.32-1.56	1.62 1.46-1.72	0.96 0.82-1.02	0.53 0.42-0.60	0.46 0.36-0.54	0.30 0.24-0.32	0.20 0.18-0.20	0.59 0.56-0.61	0.33 0.25-0.36	1.14 1.11-1.18
	F	1.40 1.20-1.72	1.73 1.44-2.16	1.00 0.88-1.28	0.57 0.50-0.70	0.51 0.42-0.64	0.29 0.24-0.38	0.20 0.18-0.24	0.58 0.56-0.61	0.33 0.32-0.35	1.12 1.08-1.19

Table 10. Lengths and proportions of legs of fifteen male and five female G. lobiferus. Ranges and means in mm.

	Sex	Fe	Ti	Ta_1	Ta_2	Ta_3	Ta_4	Ta_5	L.R.	Ta_2/Ta_3
P_1	M	1.37 1.12-1.50	1.41 1.16-1.60	2.05 1.68-2.20	1.03 0.94-1.18	0.78 0.70-0.86	0.65 0.56-0.74	0.32 0.26-0.36	1.47 1.37-1.58	1.33 1.14-1.45
	F	1.45 1.30-1.72	1.54 1.30-2.00	2.45 1.82-3.00	0.98 0.64-1.30	0.79 0.64-1.04	0.68 0.60-0.90	0.33 0.30-0.40	1.45 1.30-1.50	1.23 1.00-1.44
P_2	M	1.47 1.20-1.64	1.55 1.26-1.76	0.83 0.72-0.90	0.56 0.50-0.72	0.44 0.38-0.68	0.30 0.26-0.34	0.21 0.18-0.22	0.53 0.51-0.57	1.28 1.06-1.41
	F	1.65 1.52-1.94	1.90 1.72-2.16	1.00 0.78-1.42	0.62 0.44-0.90	0.48 0.36-0.70	0.32 0.24-0.40	0.23 0.20-0.28	0.52 0.45-0.68	1.30 1.22-1.40
P_3	M	1.57 1.36-1.76	1.90 1.62-2.24	1.26 1.10-1.44	0.80 0.70-0.94	0.62 0.54-0.76	0.38 0.34-0.44	0.22 0.20-0.24	0.65 0.63-0.69	1.28 1.21-1.41
	F	1.74 1.50-2.02	2.15 1.66-2.60	1.34 0.90-1.72	0.80 0.58-1.04	0.64 0.44-0.80	0.37 0.30-0.46	0.24 0.20-0.30	0.62 0.54-0.66	1.26 1.17-1.32

Table 11. Lengths and proportions of legs for five male and two female G. nr. paripes. Ranges and means in mm.

	Sex	Fe	Ti	Ta_1	Ta_2	Ta_3	Ta_4	Ta_5	L.R.	Ta_2/Ta_3
P_1	M	1.22 1.12-1.32	1.17 1.04-1.38	1.61 1.44-1.76	0.78 0.70-0.84	0.73 0.60-0.82	0.62 0.50-0.70	0.30 0.28-0.34	1.38 1.31-1.46	1.08 1.00-1.17
	F	1.13 1.08-1.18	1.15 1.04-1.26	1.65 1.60-1.70	0.77 0.76-0.78	0.67 0.64-0.70	0.56 0.52-0.60	0.28 0.28	1.44 1.35-1.54	1.15 1.11-1.19
P_2	M	1.31 1.20-1.46	1.40 1.26-1.54	0.70 0.66-0.74	0.46 0.40-0.50	0.36 0.32-0.38	0.27 0.26-0.30	0.20 0.18-0.22	0.50 0.48-0.52	1.25 1.21-1.32
	F	1.24 1.20-1.28	1.34 1.30-1.38	0.67 0.64-0.70	0.42 0.42	0.33 0.32-0.34	0.24 0.22-0.26	0.17 0.16-0.18	0.50 0.49-0.51	1.28 1.24-1.31
P_3	M	1.35 1.28-1.44	1.72 1.56-1.90	1.06 0.88-1.20	0.71 0.60-0.86	0.56 0.48-0.62	0.36 0.32-0.40	0.21 0.20-0.22	0.62 0.56-0.63	1.28 1.21-1.39
	F	1.32 1.26-1.38	1.70 1.62-1.78	1.01 0.96-1.06	0.63 0.62-0.64	0.51 0.50-0.52	0.31 0.30-0.32	0.20 0.20	0.60 0.59-0.60	1.24 1.23-1.24

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KEY TO THE SEVEN DEVELOPMENTAL STAGES OF G. DREISBACHI, G. LOBIFERUS AND G. NR. PARIPES

EGG

1 Eggs lime green ..... dreisbachi
Eggs light golden brown 2

2 (1) Eggs scattered at random in jelly ..... nr. paripes
Eggs in a single strand ..... lobiferus

LARVA

Instar I

1 Mean length ± 2SD of second antennal flagellomere 10 ± 1 μ ..... dreisbachi
Mean length ± 2SD of second antennal flagellomere 16 ± 3 μ ..... lobiferus[2], nr. paripes[2]

Instar II

1 Apical angle of mentum ≤ 90° (Fig. 10) ..... dreisbachi
Apical angle of mentum ≥ 100° (Figs. 26 and 42) 2

2 (1) Mean distance ± 2SD from apex of mentum to posterior ventral edge of head capsule in mid line (Fig. 51) 134 ± 12 μ ..... nr. paripes
Mean distance ± 2SD from apex of mentum to posterior ventral edge of head capsule in mid line (Fig. 51) 164 ± 10 μ ..... lobiferus

Instar III

1 Apical angle of mentum ≤ 90° (Fig. 11) ..... dreisbachi
Apical angle of mentum ≥ 100° (Figs. 27 and 43) 2

2 (1) Mean distance ± 2SD from apex of mentum to posterior ventral edge of head capsule in mid line 228 ± 25 μ . nr. paripes
Mean distance ± 2SD from apex of mentum to posterior ventral edge of head capsule in mid line 310 ± 24 μ ... lobiferus

[2]These two species cannot be separated completely in instar I (see text).

Instar IV

1 Apical angle of mentum ≤ 90° (Fig. 12) ..... dreisbachi
Apical angle of mentum ≥ 100° (Figs. 28 and 44) 2

2 (1) Mean distance ± 2SD from apex of mentum to posterior ventral edge of head capsule in mid line 365 ± 20 μ . nr. paripes
Mean distance ± 2SD from apex of mentum to posterior ventral edge of head capsule in mid line 479 ± 72 μ ... lobiferus

PUPA

1 Mace-shaped sclerotized structure on each of tergites III-VI ..... dreisbachi
Mace-shaped sclerotized structure on each of tergites II-VI 2

2 (1) Dorsal surface of maces on tergites V and VI devoid of spines (Figs. 67 and 68) ..... nr. paripes
Dorsal surface of maces on tergites V and VI with many small spines (Figs. 62 and 63) ..... lobiferus

ADULT

Male

1 Number of setae on scutellum 20-25 ..... dreisbachi
Number of setae on scutellum 30-58 2

2 (1) Number of acrostichals 17-23 ..... nr. paripes
Number of acrostichals 25-35 ..... lobiferus

Female

1 Number of setae on scutellum 19-29 ..... dreisbachi
Number of setae on scutellum 35-39 ..... nr. paripes
Number of setae on scutellum 48-74 ..... lobiferus

SEPARATION OF LARVAE, PUPAE AND ADULTS OF GLYPTOTENDIPES LOBIFERUS FROM OVERLAPPING COHORTS

In George Lake G. lobiferus has two cohorts per year; one commences about the third week in May and is completed by the end of the summer. The cohort resulting from these adults commences about the first half of August, overwinters, and starts to emerge 2-3 weeks after the ice has melted; however, as emergence continues throughout the summer, there is a mixing of larvae, pupae and adults from the consecutive cohorts.

Larvae from these overlapping cohorts can be separated from each other for much of June on the basis of their instar, since there is a one instar gap between the minimum age of the overwintering larvae and the maximum age of the new cohort larvae. Thereafter, because of the rate of development of the new cohort larvae, this gap is eliminated; however, the overlapping is restricted almost exclusively to the fourth instar.

Examination of the larvae in the overlapping instars shows that they exhibit dimorphism in colour and size. Some larvae are very dark red, while others are light red in colour. Additionally, practically all of the former are much larger than the latter. In view of these differences, and the fact that the former decrease and the latter increase in density, the colour and size differences appear to be correlated with cohort differences.

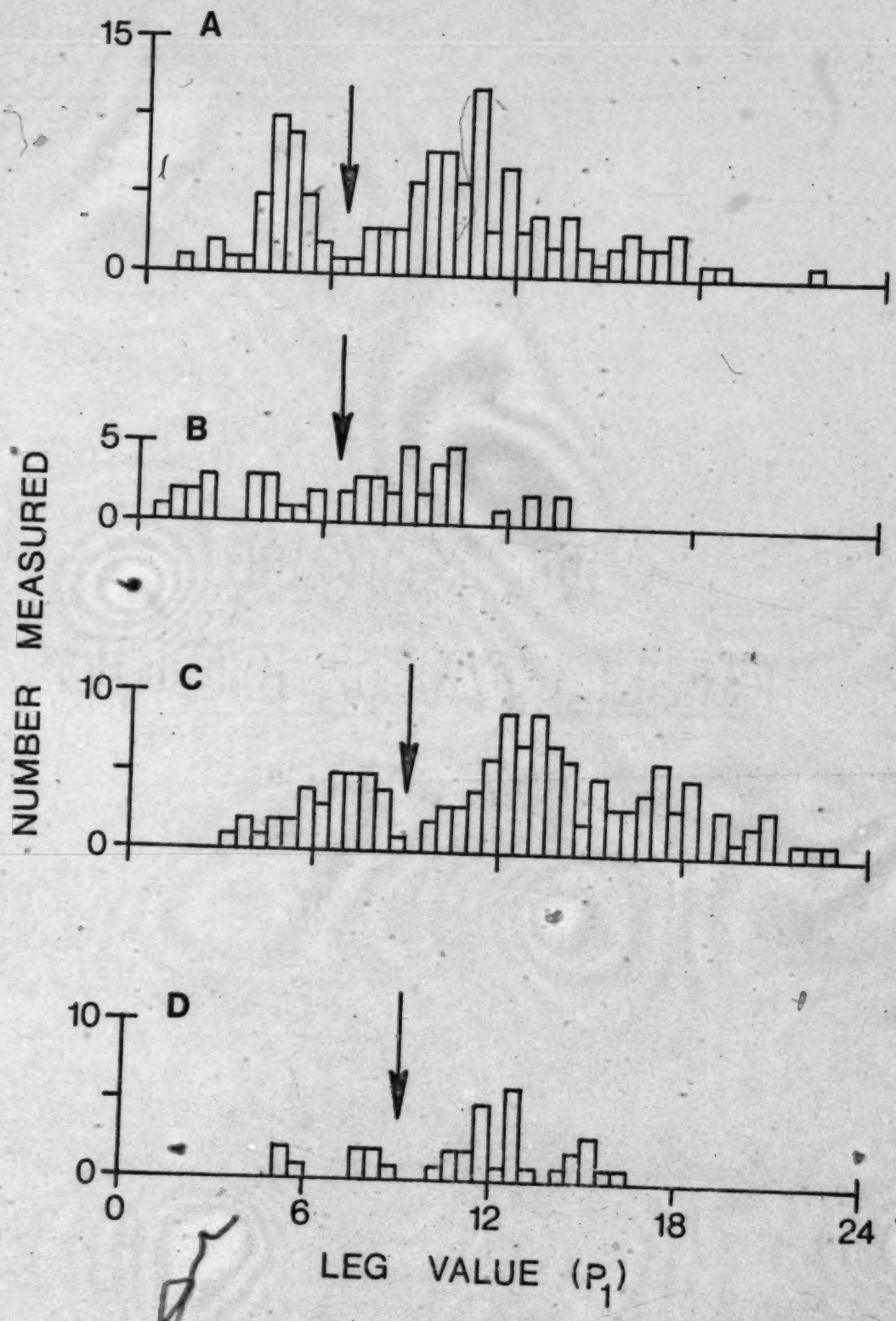
Because of the dimorphism in the larvae, pupae collected throughout the study were examined for similar differences. As all of the

pupae were preserved in 70% ethanol, measurements were made only on structures which should not be affected significantly by the preservative. Consequently, measurements were made on the length and breadth of the maces. A bimodality was obtained in the frequency distribution for each measurement, but was correlated with sexual differences. No bimodality was evident in the frequency distribution for each measurement of each sex. Because of this, and especially because of the small number of pupae collected throughout the study, it was decided to discontinue attempts to separate pupae from the overlapping cohorts.

An examination also was made of the adults for intra-sexual dimorphic characters. As all of the adults were killed and preserved in the field using 70% ethanol, measurements again were made on structures which should not be affected significantly by this technique. Consequently, measurements were made on the length of the tibia and of the first three tarsal segments of the front leg.

Comparison of the frequency distributions of the above measurements indicated bimodal distributions for the adults; however, in each measurement there was considerable overlapping in the distributions. To accentuate the difference and hence separate the frequency distributions, all of the leg measurements were multiplied together for each specimen. Frequency distributions of the resulting values are shown in Fig. 69. As can be seen, there is a clear bimodality in the values for the males from 1973 and in those from 1974 (Figs. 69A and C). Since none of the specimens constituting the frequency distributions on the left hand side of the arrows was found until the end of June in 1973 (Fig. 69A) and until the beginning of July in 1974 (Fig. 69C),

Fig. 69. Frequency distributions of the product of the length of the tibia, and first, second and third tarsal segments of the fore leg (p_1) of the males (A and C) and females (B and D) collected in 1973 and 1974 respectively. The vertical arrows represent the points separating the adults of the summer cohort (left hand side of arrows) from those of the overwintering cohort (right hand side of arrows).


A
15
0
B
5
0
C
10
0
D
10
0
NUMBER MEASURED
0
6
12
18
24
LEG VALUE (P_1)

and since most of the former specimens were collected from late July to mid-August, and most of the latter in August, these frequency distributions in all probability are composed of adults from the generation which started in May. Additional support for this is the fact that the adults constituting the frequency distributions on the right hand side of the arrows were collected first when emergence started in both years. Furthermore, most of these specimens were collected before the end of July in both years.

Although too few females adults were collected in both years to demonstrate any clear pattern, the difference in the dates of collection of those on either side of the arrows in Figs. 69C (1973) and 69D (1974) are essentially identical in both years to those recorded for the corresponding male adults.

The difference in the location of the point of division between the frequency distributions in both years can probably be attributed to differences in temperature and/or food availability to which the larvae were exposed.

The positive skew in the frequency distributions on the right hand side of the arrows for the males in both years could be a result of dormancy; the greater the delay in the date of emergence, the larger the adult, and consequently the larger the leg value. The skew also could be a result of the small sample size.

Similar to the larvae, variation in colour was noted in the adults. In general, the lighter coloured adults had shorter leg values than did the dark adults. No attempt was made to quantify these differences as the specimens had been preserved in ethanol for varying periods of time, some differing as much as one year.

APPENDIX II

CONSTRUCTION OF LIFE TABLES

INTRODUCTION

A life table is a concise summary of certain vital statistics of a population, and is a basic essential to the understanding of the population dynamics of a species. As has been pointed out by Southwood (1968), although some animal ecologists, such as Richards (1940), had expressed their results showing the successive reductions in the population of an insect throughout a single generation, Deevey (1947) was really the first to focus attention on the value of life tables.

There are two types of life tables, viz. the age-specific (or horizontal), and the time-specific (or vertical) life table. The former is based on the fate of a real cohort; conveniently the members of a population belonging to a single generation. The population may be stationary or fluctuating. The latter is based on the fate of an imaginary cohort found by determining the age structure, at a point in time, of a sample of individuals from what is assumed to be a stationary population with considerable overlapping of generations, i.e. a multi-stage population (Southwood, 1968).

For construction of a life table density estimates for the population are necessary for all developmental stages; ideally there should be several estimates for each developmental stage. Additionally, data are necessary on the fecundity and fertility of the reproductive stage.

In the present study age-specific life tables have been

constructed. The symbols used are the standard ones employed in life tables. These are:

x the pivotal age of the age class in units of time, i.e. the mid-point between consecutive sampling dates.

l_x the number of female adults surviving to reproduce during a given age interval, as a fraction of the initial number of females in the cohort. The average longevity of females has been taken as 5.5 days, and mortality was assumed to be linear with time. Additionally, egg laying has been assumed to occur one day after emergence. Thus the number of female adults surviving to reproduce during a given age interval has been taken as 81.8% of the number which emerged in that age interval (see Discussion).

m_x the age specific fertility, i.e. the number of living females born per female in each age interval. The chironomid female adults studied have been assumed to lay only one egg mass before dying; consequently m_x for each species has been taken as half the number of eggs in an egg mass (see Discussion).

V_x the multiple of l_x and m_x columns which gives the total number of female births (female eggs laid) in each age interval (the pivotal age being x).

The method of presentation of the life tables used in the present study differs from that normally encountered. Instead of just listing the pivotal age (x), a column has been included listing the actual sampling dates and the calendar age. It is believed that this

procedure makes it much easier to relate the data to seasonal phenomena and hence facilitate comparisons between the summer and winter cohorts. Estimates for the larval and adult densities are listed separately and their summation is listed under total population density. Pupae of only G. lobiferus of its first generation were found; consequently, a column for pupal density has been added in its life table (Table 18). Additionally, a column has been added for per cent cohort duration completed and one for per cent of the population surviving. These also have been added to facilitate comparisons between the various species, as there was up to a four-fold difference between them in their initial densities.

The column listing the number of females surviving to reproduce contains values which are 81.8% of the actual number of females which emerged during the specific age intervals (see definition of l_x).

No column is given for m_x as it has been assumed constant for each species (see definition of m_x).

Symbols applied to population statistics which are used in the present study include:

R_o the net reproductive rate, i.e. the number of times a population will multiply per generation. This is derived by the summation of the V_x column.

T the mean generation time. Although oviposition by females is extended over a period of time, it may be considered as concentrated for each generation at one point of time, successive generations being spaced T units apart (Dublin and Lotka, 1925). This point of time has been taken as the day by which 50% of the

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eggs have been laid. For approximate purposes T may be defined as: $T = \Sigma x\, V_x / \Sigma V_x$ (Birch, 1948). If this were an accurate estimate of T one could substitute it in the equation $r_m = \log_e R_o / T$ to calculate the intrinsic rate of natural increase. Since it is an approximation, the resulting value for the intrinsic rate of natural increase is an approximation. Laughlin (1965) proposed that this approximate value be classified as r_c and that the approximate value for the mean generation time be classified as T_c.

The value obtained for r_c is used to determine r_m (Southwood, 1968, p. 290), and the resulting value is used to determine T by substituting it in the equation $T = \log_e R_o / r_m$.

r_m the intrinsic rate of natural increase, i.e. the instantaneous growth coefficient expressed when the population is growing in an unlimited environment and the age structure has become stable. Under these conditions one solves for r_m in the equation

$$\int_o^\infty e^{-r_m x}\, l_x m_x\, dx = 1.$$

This equation can be approximated to $\Sigma e^{-r_m x}\, l_x m_x = 1$ (Southwood, 1968, p. 290).

λ the finite rate of natural increase, i.e. the number of times a population increases per unit of time. It is obtained by taking the natural antilog of r_m.

Additional information on the equations for calculating the various population statistics may be found in Southwood (1968).

REFERENCES

Birch, L.C. 1948. The intrinsic rate of natural increase of an insect population. J. Anim. Ecol., 17: 15-26.

Deevey, E.S. 1947. Life tables for natural populations of animals. Quart. Rev. Biol., 22: 283-314.

Dublin, L.I., and Lotka, A.J. 1925. On the true rate of natural increase as exemplified by the population of the United States. J. Amer. Stat. Ass., 20: 305-339.

Laughlin, R. 1965. Capacity for increase: a useful population statistic. J. Anim. Ecol., 34: 77-91.

Richards, O.W. 1940. The biology of the small white butterfly (Pieris rapae), with special reference to the factors controlling abundance. J. Anim. Ecol., 9: 243-288.

Southwood, T.R.E. 1968. Ecological methods with particular reference to the study of insect populations. Chapman and Hall, London, 391pp.

APPENDIX III

DENSITY ESTIMATES AND 95% CONFIDENCE LIMITS

INTRODUCTION

This appendix contains six tables, each of which lists the density estimates and the accompanying 95% confidence limits for the larvae of the six cohorts of the four species in each of the three sub-habitats (live and dead plant shoots, and lake bottom), and in all sub-habitats combined. For each sampling date the mean number per square meter is listed first, followed by the 95% confidence limits in parentheses.

All values listed for the mean number per square meter are arithmetic means, calculated on untransformed data. The values given for the 95% confidence limits have been derived from transformed data.

To determine the 95% confidence limits for each set of n samples (in the present study n=4), the arithmetic mean ($\bar{x}$) and the variance (s^2) were first calculated. Subsequently a Chi-Squared test was performed using the equation $X^2 = s^2 (n-1) / \bar{x}$ to check for agreement with a Poisson series. The check for agreement was made at $P \leqslant 0.05$ (Elliot, 1971, p. 42). On estimating the type of distribution pattern exhibited by the data, the appropriate transformation was chosen to normalize the data (Elliot, 1971, p. 33). The 95% confidence limits then were calculated on these normalized data. After these calculations had been made they were transformed back to the original scale. It is these final data which are listed as the 95% confidence limits.

To calculate the confidence limits for the total larval density on each sampling date the estimates for the number per square meter in each sub-habitat were summed for each of the four quadrats sampled. This gave four estimates of total larval density on each sampling date

from which the mean and the 95% confidence limits could be calculated as outlined above.

TABLE 12. Density estimates and accompanying 95% confidence limits (in parentheses) for larvae of the 1973-74 cohort of D. nervosus in each of the three sub-habitats, and in all sub-habitats combined. No samples were collected after May 8, 1974.

Date	Number Per Square Meter			
	Live Shoots	Dead Shoots	Lake Bottom	Total
June 21	3 (0-12)	19 (0-82)	0	22 (0-198)
26	3 (0-11)	46 (0-192)	0	48 (0-481)
July 1	22 (0-60)	370 (156-717)	0	391 (170-756)
6	30 (0-126)	482 (247-842)	157 (0-665)	668 (226-1535)
11	10 (0-32)	372 (88-1051)	0	382 (106-1008)
16	0	556 (153-1461)	157 (0-665)	713 (519-953)
21	59 (0-269)	547 (229-1078)	314 (0-1337)	921 (392-1803)
26	24 (0-81)	338 (192-510)	157 (0-665)	519 (173-1169)
31	7 (0-29)	281 (135-509)	157 (0-665)	445 (129-1104)
Aug. 5	44 (0-131)	342 (153-638)	0	385 (164-747)
10	18 (14-23)	335 (41-1355)	0	353 (55-1335)
15	20 (0-70)	335 (128-696)	0	355 (127-774)
20	29 (0-86)	402 (285-531)	314 (0-992)	745 (277-1614)
25	8 (0-24)	404 (310-506)	0	411 (312-530)
30	0	450 (47-1891)	157 (0-665)	607 (307-1073)
Sept. 4	11 (0-35)	439 (270-634)	157 (0-665)	606 (228-1282)
10	27 (0-113)	424 (328-492)	0	451 (382-528)
17	14 (0-48)	517 (55-1901)	0	530 (81-1702)
24	16 (0-53)	252 (148-376)	0	268 (180-383)
Oct. 1	5 (0-23)	419 (150-924)	157 (0-665)	582 (319-969)
15	52 (0-206)	670 (214-1599)	0	721 (210-1833)
Nov. 5	9 (0-38)	319 (128-639)	0	328 (139-643)
Dec. 10	3 (0-11)	174 (26-540)	0	177 (31-545)
Feb. 5	0	165 (49-400)	0	165 (50-412)
May 8	15 (0-59)	165 (15-642)	0	180 (16-817)

TABLE 13. Density estimates and accompanying 95% confidence limits (in parentheses) for larvae of the 1973 cohort of *G. dreisbachi* in each of the three sub-habitats, and in all sub-habitats combined.

Date	Number Per Square Meter			
	Live Shoots	Dead Shoots	Lake Bottom	Total
June 3	34 (0-147)	4 (0-15)	0	37 (0-427)
7	191 (12-834)	5 (0-22)	0	196 (13-1122)
13	250 (35-883)	41 (4-94)	0	292 (102-660)
17	671 (62-2035)	33 (5-72)	0	704 (89-1992)
21	169 (0-3480)	85 (4-276)	0	254 (99-1469)
26	326 (0-2796)	37 (0-156)	0	363 (5-4439)
July 1	104 (0-4862)	11 (0-47)	0	115 (0-11,935)
6	210 (74-445)	20 (0-55)	0	230 (91-467)
11	185 (92-298)	7 (0-25)	0	193 (107-318)
16	389 (12-2290)	10 (0-33)	0	399 (15-3086)
21	145 (0-2337)	8 (0-26)	0	153 (13-2010)
26	221 (48-581)	2 (0-8)	0	223 (53-600)
31	129 (91-170)	6 (0-20)	0	135 (90-194)
Aug. 5	36 (0-92)	0	0	36 (0-92)
10	36 (18-56)	0	0	36 (18-56)
15	7 (0-31)	0	0	7 (0-31)
20	19 (0-66)	0	0	19 (0-66)
25	0	0	0	0

TABLE 14. Density estimates and accompanying 95% confidence limits (in parentheses) for larvae of the 1973 cohort of G. lobiferus in each of the three sub-habitats, and in all sub-habitats combined. After August 20 the larvae of this cohort could not be differentiated accurately from those of the subsequent cohort.

Date	Number Per Square Meter			
	Live Shoots	Dead Shoots	Lake Bottom	Total
June 3	0	33 (0-158)	2200 (0-6356)	2234 (27-29,756)
7	0	134 (19-434)	472 (0-1113)	605 (22-5128)
13	16 (0-54)	446 (108-1143)	157 (0-665)	620 (182-1535)
17	16 (0-71)	447 (196-874)	0	463 (192-944)
21	4 (0-17)	449 (305-611)	157 (0-665)	610 (245-1233)
26	0	260 (0-2222)	157 (0-665)	417 (139-960)
July 1	4 (0-18)	129 (6-547)	314 (0-1337)	447 (18-2419)
6	0	190 (30-570)	629 (0-2069)	819 (18-5793)
11	0	135 (9-507)	314 (0-992)	449 (111-1254)
16	0	159 (109-216)	629 (0-2069)	788 (53-3827)
21	0	86 (29-159)	157 (0-665)	243 (21-900)
26	3 (0-12)	77 (13-171)	157 (0-665)	238 (13-1100)
31	6 (0-20)	87 (29-163)	0	94 (33-211)
Aug. 5	4 (0-15)	120 (42-257)	0	124 (46-268)
10	5 (0-21)	58 (5-185)	0	63 (9-235)
15	0	37 (0-407)	0	37 (0-407)
20	0	10 (0-58)	0	10 (0-58)

TABLE 15. Density estimates and accompanying 95% confidence limits (in parentheses) for larvae of the 1973-74 cohort of G. lobiferus in each of the three sub-habitats, and in all sub-habitats combined. No samples were collected after May 8, 1974.

Date	Number Per Square Meter			
	Live Shoots	Dead Shoots	Lake Bottom	Total
Aug. 5	23 (0-85)	110 (0-623)	0	133 (0-2707)
10	0	57 (0-630)	0	57 (0-630)
15	33 (0-147)	142 (30-389)	0	175 (44-494)
20	18 (0-61)	727 (210-1955)	0	745 (251-1765)
25	57 (4-168)	815 (497-1252)	0	872 (520-1364)
30	52 (10-111)	740 (160-2024)	0	791 (209-1977)
Sept. 4	133 (54-234)	1057 (700-1530)	0	1191 (764-1769)
10	151 (14-565)	1036 (661-1536)	0	1186 (815-1660)
17	72 (0-314)	827 (210-2103)	0	899 (311-1956)
24	145 (0-792)	917 (294-2101)	157 (0-665)	1219 (675-2002)
Oct. 1	48 (0-189)	811 (257-1904)	0	859 (264-2069)
15	92 (10-536)	905 (552-1392)	0	996 (570-1612)
Nov. 5	22 (0-75)	514 (174-1182)	0	536 (202-1156)
Dec. 10	52 (11-108)	407 (383-431)	0	459 (421-498)
Feb. 5	26 (0-77)	430 (282-599)	157 (0-665)	613 (340-1008)
May 8	126 (12-444)	499 (221-964)	0	625 (335-1056)

TABLE 16. Density estimates and accompanying 95% confidence limits (in parentheses) for larvae of the 1973 cohort of G. nr. paripes in each of the three sub-habitats, and in all sub-habitats combined. After August 20 the larvae of this cohort could not be differentiated accurately from those of the subsequent cohort.

Date	Number Per Square Meter			
	Live Shoots	Dead Shoots	Lake Bottom	Total
June 3	0	13 (0-44)	2515 (0-6832)	2528 (23-43,390)
7	0	78 (0-398)	1100 (0-3763)	1179 (30-8174)
13	0	236 (119-417)	943 (0-3867)	1180 (77-5095)
17	8 (0-35)	232 (54-656)	629 (0-2069)	869 (146-2850)
21	4 (0-17)	228 (141-327)	0	232 (146-349)
26	10 (0-36)	208 (52-533)	0	219 (58-571)
July 1	12 (0-53)	149 (64-255)	472 (0-1578)	633 (77-2317)
6	11 (0-48)	130 (25-369)	472 (0-1578)	613 (79-2296)
11	5 (0-21)	117 (6-530)	472 (0-2012)	594 (32-2363)
16	0	213 (129-311)	472 (0-2012)	685 (74-2236)
21	0	208 (88-360)	314 (0-1337)	523 (47-1906)
26	34 (0-151)	104 (50-171)	314 (0-992)	453 (93-1360)
31	0	112 (68-173)	0	112 (68-173)
Aug. 5	6 (0-27)	81 (42-127)	0	87 (54-132)
10	0	52 (0-665)	0	52 (0-665)
15	7 (0-31)	25 (0-78)	0	33 (0-296)
20	0	24 (7-59)	0	24 (7-59)

TABLE 17. Density estimates and accompanying 95% confidence limits (in parentheses) for larvae of the 1973-74 cohort of G. nr. paripes in each of the three sub-habitats, and in all sub-habitats combined. No samples were collected after May 8, 1974.

Date	Number Per Square Meter			
	Live Shoots	Dead Shoots	Lake Bottom	Total
July 31	0	6 (0-40)	0	6 (0-40)
Aug. 5	27 (0-93)	115 (5-500)	0	143 (7-895)
10	10 (0-33)	68 (25-123)	0	79 (45-125)
15	22 (0-97)	99 (22-265)	0	121 (26-373)
20	22 (0-55)	372 (135-822)	0	394 (162-811)
25	63 (4-151)	466 (233-824)	0	529 (257-959)
30	30 (0-85)	373 (100-934)	0	403 (108-1045)
Sept. 4	67 (13-142)	556 (360-816)	0	623 (408-910)
10	72 (0-195)	616 (348-1001)	0	688 (401-1094)
17	18 (0-44)	510 (192-1055)	0	528 (206-1078)
24	94 (0-451)	535 (232-1024)	0	629 (272-1226)
Oct. 1	52 (0-209)	422 (120-1073)	0	474 (133-1226)
15	88 (0-429)	467 (348-597)	0	555 (395-755)
Nov. 5	10 (0-32)	279 (135-506)	0	289 (134-546)
Dec. 10	46 (18-81)	251 (172-336)	0	296 (242-359)
Feb. 5	14 (0-50)	221 (107-360)	0	235 (137-371)
May 8	44 (10-89)	257 (79-498)	0	301 (117-637)

REFERENCES

Elliot, J.M. 1971. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biological Association, Sci. Publ. No. 25, 144pp.